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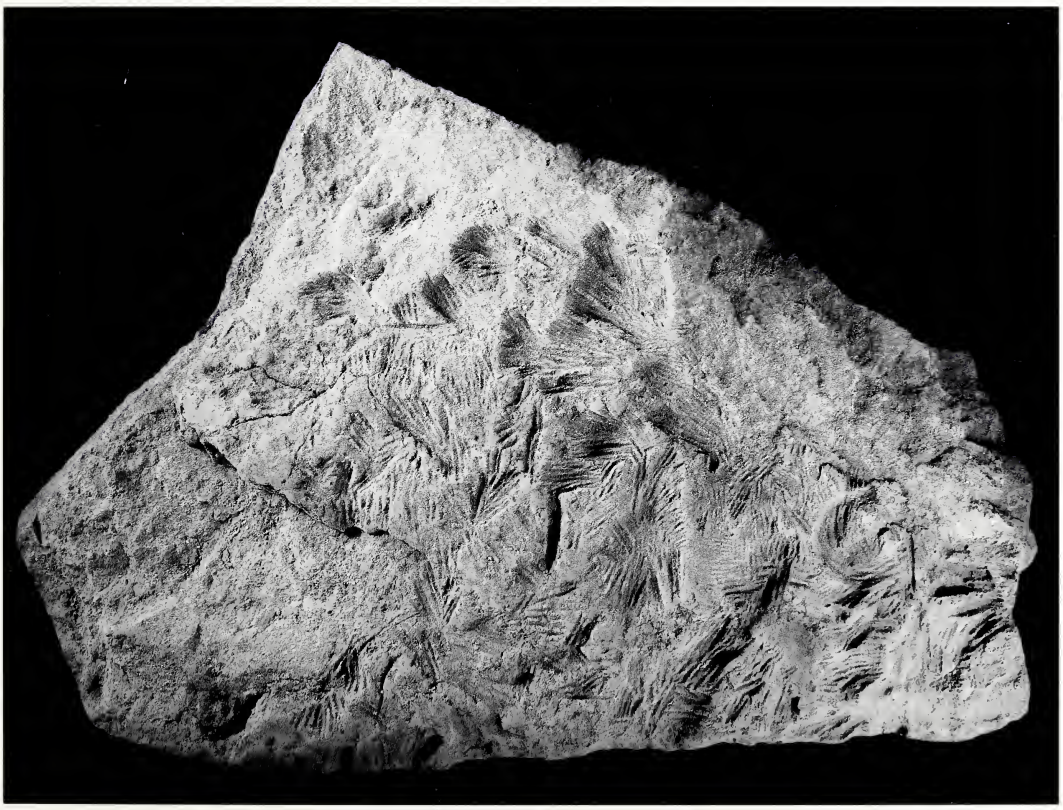

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Cover photo: A carbonate rock gnawed by rodents, leaving characteristic tooth marks on the rock. The marks show the scoop-like U-shaped cross section typical of rodent incisors. Size of the marks indicates that they were made by rodents ranging from mouse-sized species to rabbits. (*See related paper on page 1.*)

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RODENT-GNAWED CARBONATE ROCKS FROM INDIANA

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ABSTRACT. Two carbonate-rock specimens from Jasper County and Monroe County, Indiana, are marked superficially by numerous grooves left by lower incisors of modern rodents. The Jasper County specimen is a calcitic dolomite, with incisor marks most closely matching size ranges for *Sciurus* (?)*carolinensis* (gray squirrel), *Tamias striatus* (eastern chipmunk) and mouse-sized species. The Monroe County specimen is dolomitic limestone showing marks in the size range of *Sciurus niger* (fox squirrel), *Marmota monax* (woodchuck), mouse-sized species, and possibly the lagomorph *Sylvilagus floridanus* (eastern cottontail). Both rocks contain an abundance of calcium, magnesium and clay minerals which may have been a source of nutrients for the rodents, but also contain significant amounts (*ca.* 20%) of SiO_2 (quartz), which may act as a fine abrasive for wearing down ever-growing incisors. Weathering has softened the surface of both rock samples, thus facilitating the gnawing activity and perhaps explaining why several different species selected these particular rocks upon which to gnaw. It is also possible that once rodents had gnawed and deposited their scent on the rocks, other rodents would be attracted to inspect and gnaw the rocks in turn. However, there is as yet no record of such behavior among Indiana rodents.

Keywords: Gnaw marks, rodents, Ramp Creek, Rockford Limestone.

It is well-known that members of the Order Rodentia, whose name translates to "the gnawers," will chew on bones in the wild, and that "pest" species, such as *Mus musculus* (house mouse), chew through wood, plastic and many other materials they encounter. By comparison, the gnawing of rocks by rodents is rarely observed. Cuffey & Hattin (1965) reported gnawing of chalk by *Sylvilagus audobonii* (desert cottontail); and Gow (1992) observed African porcupines, presumably *Hystrix,* gnawing a siltstone ledge. Apart from these references, few or no studies have focused on rock-gnawing and its importance. Samples of carbonate rock from two Indiana counties situated about 200 km apart show significant modification of rock surfaces by rodent gnawing. The marks were probably produced within a few years' time because, in the Indiana climate, limestone erodes readily with exposure to the elements; and such marks are likely to be dulled or obliterated within a relatively short time.

Gnaw marks appear as paired, in some places divergent, grooves of wide-ranging size. The marks show the scoop-like, U-shaped cross-section typical of lower incisors rather than the flat-edged cross-section left by upper incisors (Burns et al. 1989). Imprints of upper teeth, left when the rodent braces its upper incisors against the gnawed surface (Burns et al. 1989), are not preserved. In rodents, the mandibular symphysis between the lower incisors spreads as the jaw muscles contract. This causes the teeth to diverge and function as tweezers, and enables the rodent to scrape around corners, so that the lower incisors are more maneuverable than the uppers and are the pair most often used to gnaw. Rodents which burrow through hard-packed soils use lower incisors rather than uppers (Burns et al. 1989; Zuri et al. 1999), so lower incisors are more likely to be used on hard rock. The Indiana samples suggest gnawing activity by more than one rodent species, as the tooth marks vary greatly in size. This study is aimed at identifying tooth marks to rodent taxa, and investigating whether rodents gnaw for nutritional purposes, for wearing down their teeth, or both, and whether gnawing is a response to local environmental conditions or implies more widespread behavior and physiological needs.

METHODS

To identify rodent taxa which might have produced the tooth marks on the Jasper and Monroe County carbonate-rock samples, widths of various-sized single and paired grooves were measured on each sample and compared with lower incisor widths from several species of rodents and lagomorphs known to be common in these counties. Rare taxa, or those with incisor widths well outside the range suggested by the tooth marks on the rocks, were not included. Mandibles from Indiana species were placed directly against the tooth marks on the rocks to find an approximate size match before they were measured. Skeletal specimens used in this study are part of the mammal collections in the Zooarchaeology Laboratory at Indiana University Bloomington, with the exception of one *Marmota monax* skull from the Division of Mammals in the University of Kansas Natural History Museum. Incisors were measured in place in alveoli, and each tooth or pair of teeth was measured as close to the occlusal (gnawing) edge as possible. All measurements were made to the nearest 0.1 mm with dial calipers.

Mandible specimens used were as follows; they are in the Indiana University Bloomington Zooarchaeology Laboratory unless otherwise specified. "IU" refers to Indiana University Bloomington; "KU" refers to the Division of Mammals, University of Kansas Natural History Museum. The specimens were: *Marmota monax:* IU 901152, 9310936, 9510208, 9610169, 9710153, A3, A51, AA32, BB16, M1, M6, K23, K76, S83, S94, T22; KU RMT4126. *Sciurus niger:* IU 84152, 84154, 84156, 84159, 841119, 841146, 8410067, 921225, 9110587, 9310582, 9310595, 9810182, HH76; immature specimens IU 369, 891382, 891383, 9610128, EE7. *Sciurus carolinensis:* IU 84122, 84124, 9610225, 9610226, D72, J16; immature specimens IU 9710476, M26. *Tamias striatus:* IU 84141, 9710371, EE61, W98, also one unnumbered specimen; immature specimen IU DD20. *Rattus norvegicus:* IU AA54; *Peromyscus maniculatus:* IU S91; *Peromyscus leucopus:* IU 9810007; *Zapus hudsonicus:* IU FF79.

RESULTS

Description of rock samples.—Specimens of rodent-gnawed rock which are the principal basis for this study consist of impure, fine-grained carbonate rocks, including one sample from the lower Mississippian Rockford Limestone and one from the middle Mississippian Ramp Creek Formation. The Rockford specimen is a much-weathered, mostly dark yellowish-orange (10 YR 6/6 on Geological Society of America Rock-color Chart) calcitic dolostone, as determined from acid-reaction tests (Low 1951), thin sections, and x-ray diffraction analysis. This rock has a primarily microcrystalline texture, with grayish-colored patches of micrite which do not react to alizarin red S solution. A small part of the rock comprises coarsely crystalline calcite containing abundant silt and very fine sand-sized dolorhombs. Accessory components include silt-sized quartz (SiO_2) grains, which are locally abundant, and silicified skeletal remains derived primarily from crinoids that are scattered irregularly throughout. A small sample of this specimen was digested in hydrochloric acid (HCl), producing an insoluble residue amounting to 21.17% of the rock. X-ray diffraction analysis of the residue shows quartz as the dominant residue component, with scarcely more than trace quantities of magnesium calcite $(Ca, Mg)CO_3$ and the clay mineral illite $(KAl_2(OH_2).[AlSi_3(O,OH)_{10}])$. This specimen, which is almost completely covered with tooth marks (Fig. 1), was collected by N. Gary Lane from a ditch near the center of section 21, T 27N, R 7W, Jasper County, Indiana. The locality and rock section are described by Gutschick & Treckman (1957).

The Ramp Creek sample is a moderate yellowish-brown (10 YR 5/4) dolomitic limestone as determined by the same testing methods used on the Rockford sample. This rock has a very fine grained microsparry matrix, in which are scattered very fine sand- and silt-sized rhombs of dolomite ($MgCO_3$), mostly silt-sized angular grains of quartz, and sand- to very fine gravel-sized skeletal grains derived from crinoids. The skeletal grains retain their calcitic composition, as determined from optical and staining techniques. As with the Rockford sample, a small portion of this sample was digested in hydrochloric acid, producing an insoluble residue representing 20.59% of the original rock. X-ray diffraction analysis of the residue shows quartz as the overwhelmingly predominant residue component, with little more than trace quantities of magnesium

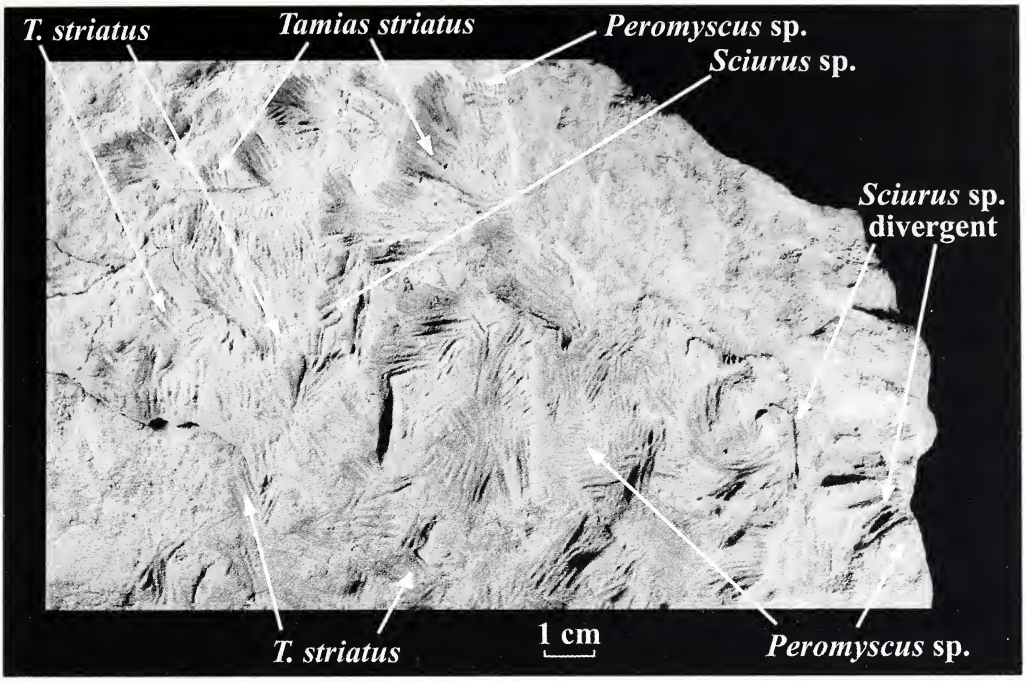

Figure 1.—Rockford Limestone slab (lower Mississippian) from Jasper County, Indiana, showing numerous marks left by rodent lower incisors. Labels denote best-preserved sets of tooth marks, with approximate identification of rodent species.

calcite, illite, and kaolinite ($Al_2Si_2O_5(OH)_4$), in decreasing order of abundance. The Ramp Creek sample was collected in 1984 by former Indiana University student David Kring from a Monroe County locality believed to be at the east edge of Bloomington, Indiana, near the intersection of State Road 45 and Smith Road.

The Jasper County specimen measures 18.4 cm long and 29.8 cm wide, with roughly 50% of one surface marked by small, paired scrape- or groove-like tooth marks (Fig. 1). Gnawed portions and other relatively fresh surfaces are dark yellowish-orange, whereas more weathered portions appear yellowish-gray. The rock is soft, crumbling away slightly with handling so as to leave orange-colored dust on the fingers, and is easily scratched with a fingernail.

On the Jasper County specimen, paired gnaw-marks display a wide range of sizes. At least two sets of marks on this and the Monroe County sample diverge along their length, indicating the spreading of the mandibular symphysis (Fig. 1). Width of single tooth marks ranges from 0.2–1.1 mm, with a majority of marks being 0.9–1.0 mm across (Table 1). Width of paired marks ranges from 1.3–3.3 mm, with most pairs approximating 2.2 mm. Comparison with tooth measurements averaged for each Indiana rodent species suggests that 50% of measured marks correspond to lower incisor width of some species of *Sciurus*, possibly *S. carolinensis* (gray squirrel), incisor width, whereas about 25% match lower incisors of *Tamias striatus* (eastern chipmunk). There is one group of small tooth marks of *ca.* 0.5–0.9 mm single and 1.2–1.5 mm paired width (Fig. 1; Table 1) that appear to match tooth size of smaller Indiana rodents, such as *Peromyscus maniculatus* (deer mouse), *Peromyscis leucopus* (white-footed mouse), *Zapus hudsonicus* (meadow jumping mouse), *Microtus pennsylvanicus* (meadow vole), *Microtus orchrogaster* (prairie vole), *Microtus pinetorum* (woodland vole) and *Mus musculus* (house mouse).

The limestone specimen collected from Monroe County, Indiana is smaller than the Jasper County specimen, measuring 12.0 cm in length and 9.6 cm in width (Fig. 2). A rough sketch, presumably made by the collector, accompanies the specimen and indicates

Table 1.—Comparison of lower incisor widths measured from skeletal specimens with widths of tooth marks on Indiana carbonate rock specimens. The number of marks measured represents the best-preserved sets of marks on each rock, and does not necessarily reflect total number of marks of that size. Because tooth mark widths are approximate owing to imperfect clarity, identifications of rodent species are also estimates. All measurements are in mm.

Rock specimen	Rodent species	Range, single incisor width	Range, paired incisor width	Number of tooth marks	Range, single tooth mark	Range, paired tooth marks
Rockford Limestone (Jasper County)	*Marmota monax* (woodchuck)	2.1–4.1	4.9–9.7	5	3.4–3.8	5.5
	Sciurus niger (fox squirrel)	1.0–1.8	2.4–4.1	5	0.9–1.8	3.4–4.4
	Tamias striatus (eastern chipmunk and/or mouse-sized species)	0.4–1.1	1.3–2.6	2	0.6–0.9	1.7
Ramp Creek Formation (Monroe County)	*Sciurus carolinensis* (gray squirrel)	0.8–1.3	1.8–3.1	16	1.0–1.1	1.8–3.0
	Tamias striatus	0.4–1.1	1.3–2.6	8	0.8–0.9	1.8–2.4
	Peromyscus leucopus (white-footed mouse or *P. maniculatus* deer mouse)	0.7	1.2	4	0.7	1.2–1.5
	Zapus hudsonicus (meadow jumping mouse)	0.4	1.3	5	0.3–0.5	1.2–1.5

that the gnawed sample was collected on a steep slope beneath an overhanging ledge of bedrock. Tooth marks occur only on one side of the rock specimen and cover about 75% of that surface (Fig. 2).

This sample is comparable to the Jasper County specimen in texture, fossil content, and relative hardness, but the surface appears to have been scraped nearly smooth by gnawing, and the rock is less crumbly than the Jasper sample. The gnawed surface is less weathered than in the Jasper County sample, and tooth marks are comparatively larger. Approximately 35% of measured marks are ca. 1.8–2.0 mm single and 3.4–5.5 mm paired width and correspond most closely in size to *Sciurus niger* (fox squirrel) incisors. Another 35% of measured marks are relatively large, *ca.* 3.4–4.8 mm single and 5.5 mm paired width, and match *Marmota monax* (woodchuck) incisors (Table 1). Smaller marks of *ca.* 0.6–0.9 mm single and 1.7–2.1 mm paired width (Fig. 2) may be from smaller fox squirrel individuals and from smaller, mouse-sized species, as in the Jasper County specimen. One pair of marks appears to show a central groove (Fig. 2), which may correspond to the upper incisors of a lagomorph (see Cuffey & Hattin 1965). *Sylvilagus floridanus* (eastern cottontail) is the most likely species to occur in Monroe County, and may have produced this pair of marks.

Identifications of gnawing taxa for the two Indiana carbonate-rock specimens are estimates at best. Some of the marks measured in this study fall into the size range of *Sylvilagus floridanus* lower incisors, which would look exactly like rodent incisor marks because they lack the central groove of rabbit upper incisors. However, aside from one set of marks on the Monroe County specimen described above, none of the marks shows distinct central grooves, and all are assumed to have been made by rodents. Unequivocal correlation of species to tooth marks is probably impossible, as the soft, crumbly limestone does not provide sharp distinction of marks; and many Indiana rodents share roughly the same range of tooth size. Additional research, such as live-trapping or analysis of carnivore scat and owl pellets from the two specimen localities could provide a cross-section of local rodent populations and aid in identification of tooth marks.

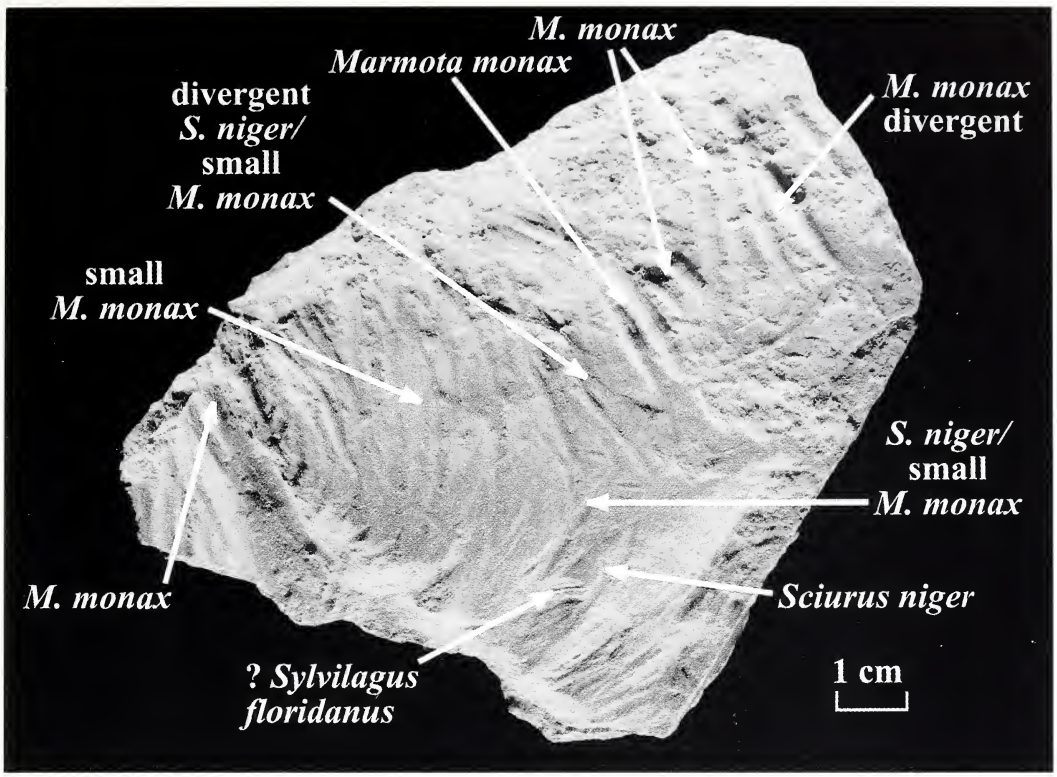

Figure 2.—Ramp Creek limestone specimen (middle Mississippian) from Monroe County, Indiana, with best-preserved tooth marks denoted by labels and with approximate identifications of species. Note central grooves in tooth marks identified as possibly those of the eastern cottontail.

Preliminary observations of rock-gnawing.—Three female *Rattus norvegicus* (domestic Norway rats – relatively recent immigrants to the United States) were kept to see whether captive rodents will gnaw on rocks, and if so, how often. The rats were approximately three weeks old when obtained. They were fed a diverse diet, including fruits, vegetables, grain cereal and rat pellets. If gnawing on various foods is sufficient to wear down incisors, as implied in Zuri et al. (1999), rat pellets and seeds are hard enough to serve this purpose for captive rodents. The pellets are also fortified with vitamins and minerals, including $CaCO_3$, so that the rats' diet had no severe deficiencies. One piece each of the Jasper and Monroe County rock specimens was placed in the rats' cage. Within the first few weeks, the rats left tooth marks on both rocks.

Gnawing occurred at night, for the rats slept throughout the day and were never observed gnawing the rocks. They gnawed selectively on corners and along edges of the specimens. On the Jasper sample they gnawed heavily on one relatively weathered side, and not at all on the other sides. After these first few weeks, no more new tooth marks were visible, and the rock surfaces which had been gnawed began to wear smooth from the rats' climbing over the rocks. Whereas they stopped gnawing the rocks, the rats often grated their upper incisors against the lowers, a habit common among caged rodents, and probably wild ones, that serves to hone the incisors and keep them worn down (Howard & Smith 1952). They also gnawed the bars of the cage.

In May 1999, a piece of Plattsmouth Limestone from the University of Kansas campus in Lawrence was placed against the wall of an apartment building just outside of campus, to see whether any wild rodents would chance to come and gnaw on it. Within a few days, a row of tiny tooth marks was observed along one sharp edge of the rock (Fig. 3). The tooth marks are in the size range of such small rodents as *Peromyscus leucopus* and *Mus mus-*

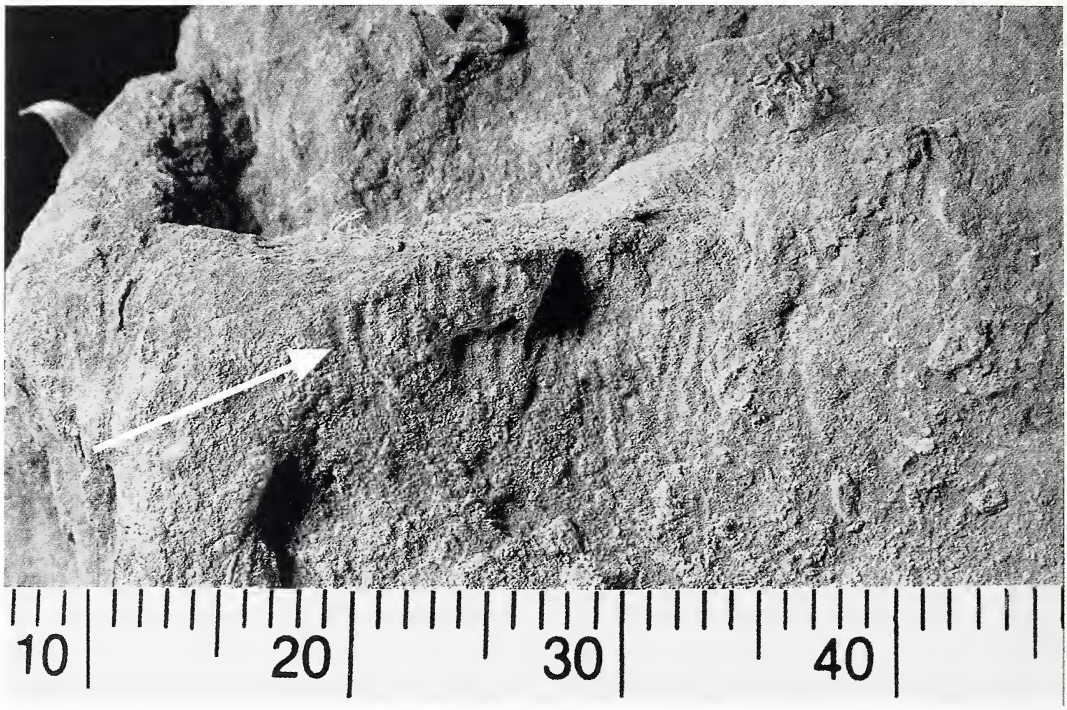

Figure 3.—Sample of Plattsmouth Limestone (Pennsylvanian) from the University of Kansas campus, showing tooth marks left by a mouse-sized rodent.

culus, two species likely to live near human dwellings (Mumford & Whitaker 1982).

DISCUSSION

Rock-gnawing by rodents may be more common than has been assumed. Unless rodents gnaw repeatedly at one specific rock, their tooth marks are likely to be dispersed among many rocks and easily missed, especially if they are quickly erased by weathering. However, rock-gnawing is occasionally observed in the wild as a routine event. Karl W. Leonard (pers. commun. 1997) reported several instances in which *Sciurus niger* gnawed on Silurian Lockport Limestone at a corner of the Geology building on the campus of Kansas State University in Manhattan, Kansas. It is possible that the rock samples from Indiana were likewise visited on separate occasions.

Based upon preliminary observations, captive *Rattus norvegicus* gnaw preferentially along edges and on freshly exposed, relatively crumbly surfaces. Although rock and other hard substances abrade rodent incisors quickly (Burns et al. 1989), the fact that the rats barely used the rock for a long period of time indicates that it was not needed to grind down incisors, at least not on a regular basis. This is particularly evident because, assuming that these activities are to wear down teeth and are not simply due to boredom, the rats continued to gnaw the cage bars and grate their teeth long after they stopped using the rock. Whether only one individual rat produced all the tooth marks, or whether gnawing activity to obtain calcium or magnesium would increase due to pregnancy and/or lactation, are among questions remaining to be addressed using captive rats. Whether the piece of Plattsmouth limestone sample placed outdoors and gnawed by a wild, mouse-sized rodent was simply put in a convenient spot, or attracted the rodent for physical or nutritional needs, remains uncertain.

Rodents may gnaw on rocks for various reasons, including need for minerals, need to wear down the teeth, or need to release stress. Several records show that rodents, lagomorphs and artiodactyls derive minerals directly from rocks. *Sciurus niger* and *Marmota*

monax, both of which may have produced tooth marks on the Indiana rocks, are known to lick salt (NaCl) from roadsides during springtime in southern Indiana (Weeks & Kirkpatrick 1978; Mumford & Whitaker 1982). Presumably, however, the only minerals a rodent could obtain from the Jasper and Monroe County specimens are calcium, magnesium and possibly the clay minerals illite and kaolinite. *Sylvilagus floridanus* may eat clay soil on occasion (Mumford & Whitaker 1982), and *Sylvilagus audobonii* is known to have gnawed extensively on Ca-rich but Si-poor chalky limestone (Cuffey & Hattin 1965). *Neotoma floridana* (wood rat), *Hystrix* sp. (African porcupine) and *Geomys bursarius* (eastern pocket gopher) store and gnaw on bones, most likely to gain calcium, sodium, and phosphorus (Smith 1948; Duthie & Skinner 1986; Richards & Munson 1988; Gow 1992). Small rodent gnaw marks are common on accumulated fossil bones in deposits such as sinkholes, which suggests that rodents specifically seek calcium and other minerals for certain dietary needs.

The Jasper and Monroe County rocks are dominated by the minerals calcite ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$) and would be good sources of calcium and magnesium, thus possibly functioning as rodent "licks" similar to those reported by Jones & Hanson (1985) and Peterson (1955) for artiodactyls. Deer and elk licks, in particular, are rich in calcium and magnesium, which are leached from limestones into the soil (Jones & Hanson 1985). However, studies on *Sciurus niger* and *Marmota monax* in southern Indiana (Weeks & Kirkpatrick 1978) show that these species seek sodium much more frequently than they seek calcium and magnesium.

Nutritional needs probably vary among species, individuals and environments. For example, "salt drives" in *Sciurus niger* and *Marmota monax* are highest in springtime (Weeks & Kirkpatrick 1978). Calcium and magnesium may also be more sought after in springtime. Plants growing in carbonate soils, such as those which occur abundantly in Indiana, are naturally enriched in calcium (Jones & Hanson 1985), and perhaps in magnesium. *Marmota monax* eats mainly leaves and stems of plants and may derive much of the calcium and magnesium in its diet from those plants during their growing season. Upon emerging from hibernation in early spring when plants are scarce, *M. monax* may have a calcium/magnesium deficiency which could be compensated for by gnawing carbonate rocks. *Sciurus niger* is not primarily a plant-eater, yet it and *Tamias striatus* may still have calcium/magnesium deficiencies during the winter and early spring months. In addition, gravid or lactating females and growing juveniles may require larger amounts of these minerals than other individuals.

Alternatively, rodents gnawed the Indiana rocks to help wear down continually growing incisors. Observations of captive *Rattus norvegicus* seem to suggest that a rock is not required to wear down teeth on a routine basis, if the rodent habitually eats hard foods. Cuffey & Hattin (1965) discount gnawing to wear down teeth based on the softness of their gnawed chalk sample, which contained only about 1% SiO_2. On the other hand, Gow (1992) observed *Hystrix* sp. gnawing on siltstone containing >1% calcium, which was "like a soft talc" and "easily scored by a fingernail," and suggested that the siltstone could serve as a fine abrasive polish for teeth. Limestone typically has a hardness of about 3. The enamel of rodent incisors contains iron and is therefore harder than the enamel of most mammal teeth. Thus, most carbonate rocks are probably too soft to wear down rodent incisors appreciably. However, as the Indiana samples contain *ca.* 20% SiO_2, they may provide a fine abrasive to help hone incisors. In any case, rodents gnawing these Indiana rocks probably subjected their lower incisors to wear, due to the relatively great amount of SiO_2 in the samples.

Why several different species selected the same Rockford and Ramp Creek samples for gnawing is an intriguing question. Both specimens have suffered considerable weathering such that the rock surfaces are soft and somewhat crumbly. Such a condition would make gnawing, especially for nutrients, an easy process and could explain why more than one species chose each of these rocks for its nutritional or tooth-wear needs. It is also probable that, once a rodent had gnawed and left its scent on the rock exposure, conspecifics and other species would be likely to approach the rock so as to leave their scent as well and gnaw at the rock, which would be covered with salty deposits from the other rodents.

Thus far, no studies of this type of behavior have been made; and further study is needed to determine the reasons why wild rodents gnaw on rocks, and the role carbonate rocks play in the ecology of Indiana rodents.

CONCLUSIONS

A dolomitic limestone sample from Monroe County and a calcitic dolostone sample from Jasper County, Indiana, were gnawed extensively by several species of rodents and possibly one lagomorph. Species identified to tooth marks on the rocks include *Marmota monax*, mouse-sized species, and possibly *Sciurus niger* and *Sylvilagus floridanus* (Monroe County specimen), and *Sciurus ?carolinensis*, *Tamias striatus* and mouse-sized species (Jasper County specimen). The reason for the gnawing behavior is still uncertain. We propose that the gnawed carbonates could have served as a source of calcium and/or magnesium. The rocks also contain significant amounts of abrasive SiO_2, which could help wear down rodent incisors. These needs may vary with specific habitat conditions, and further studies may demonstrate use of cacium and magnesium by pregnant or lactating rodents and rodents in seasonally or perpetually mineral-deficient areas. Preliminary observations show that both captive and wild small rodents readily gnaw on carbonate rocks placed in their environment. The rock-gnawing habit may thus extend to rodents in a wide variety of habitats, be a more common behavior than previously supposed, and be worthy of future experimental investigation.

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LITERATURE CITED

Burns, J.A., D.L. Flath & T.W. Clark. 1989. On the structure and function of white-tailed prairie dog burrows. Great Basin Naturalist 49(4):517–524.

Cuffey, R.J. & D.E. Hattin. 1965. Kansas chalk gnawed by desert cottontail. Journal of Mammalogy 46(4):696–697.

Duthie, A.G. & J.D. Skinner. 1986. Osteophagia in the Cape porcupine *Hystrix africaeaustralis*. South African Journal of Zoology 21:316–318.

Gow, C.E. 1992. Gnawing of rock outcrop by porcupines. South African Journal of Geology 95(1/2):74–75.

Gutshick, R.C. & J.F. Treckman. 1957. Lower Mississippian cephalopods from the Rockford Limestone of northern Indiana. Journal of Paleontology 31(6):1148–1153.

Howard, W.E. & M.E. Smith. 1952. Rate of extrusive growth of incisors of pocket gophers. Journal of Mammalogy 33(4):485–487.

Jones, R.L. & H.C. Hanson. 1985. Mineral Licks, Geophagy, and Biogeochemistry of North American Ungulates. The Iowa State University Press, Ames. 301 pp.

Low, J.W. 1951. Examination of well cuttings. Quarterly of the Colorado School of Mines 46(4). 48 pp.

Mumford, R.E. & J.O. Whitaker. 1982. Mammals of Indiana. Indiana University Press, Bloomington. 490 pp.

Peterson, R.L. 1955. North American Moose. University of Toronto Press, Toronto. 280 pp.

Richards, R.L. & P.J. Munson. 1988. Flat-headed peccary (*Platygonus*) and recovered Quaternary vertebrate fauna of Indun Rock Shelter, Monroe County, Indiana. National Speleological Society Bulletin 50:64–71.

Smith, C.F. 1948. A burrow of the pocket gopher (*Geomys bursarius*) in eastern Kansas. Transactions of the Kansas Academy of Science 51:313–315.

Weeks, H.P., Jr. & C.M. Kirkpatrick. 1978. Salt preferences and sodium drive phenology in fox squirrels and woodchucks. Journal of Mammalogy 59(3):531–532.

Zuri, I., I. Kaffe, D. Dayan & J. Terkel. 1999. Incisor adaptation to fossorial life in the blind mole-rat, *Spalax ehrenbergi*. Journal of Mammalogy 80(3):734–741.

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2002. Proceedings of the Indiana Academy of Science 1:9–20

SUBSURFACE INVESTIGATIONS OF SEVERAL GLACIAL SUCCESSIONS RELATED TO ENGINEERING CONSTRUCTION

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ABSTRACT. Glacial environments, including subglacial, supraglacial and proglacial deposition, yield some of the most complex sedimentary deposits on Earth. Unsorted deposits of clasts in a finer matrix (diamictons) are common, both in flow tills and basal (or lodgement) tills. Using only hand-sized samples these till varieties are difficult to differentiate and may require extensive field investigation to do so. Stratigraphic detail of glacial deposits has a profound influence on the engineering properties of soil units. Geotechnical studies involve subsurface drilling and sampling, typically using Hollow Stem Auger (HSA) and Standard Penetration Test (SPT) methods. Other soil samples are obtained using pushed Shelby tubes. Standard laboratory tests are typically performed on soil samples to determine their engineering properties relative to the geologic conditions and the type of facility to be constructed. Four sites were selected for evaluation, ranging from simple glacial stratigraphy to a complex glacial succession requiring gamma ray logging to decipher details. Till features and various types of outwash are considered regarding two engineering construction objectives: foundations for buildings and sanitary landfill siting.

Keywords: Glacial geology, subsurface investigation, engineering geology, geotechnical engineering

Much of the Upper Mississippi River Valley and Great Lakes was repeatedly covered by massive continental glaciers during the Pleistocene Epoch. When the ice melted, layers of eroded materials were deposited, with younger layers overlapping older ones. This glacial debris (unsorted clay, silt, sand, and rock fragments) was either deposited directly by the melting ice or carried away to be deposited by streams formed from meltwater. As the source of glaciers shift with time and climatic conditions differ among regions, deposits from various glaciers differ in their physical and mineralogical properties. These details can be used to distinguish between individual glacial units.

Various glacial deposits exhibit a range of properties related to their potential use and limitations for geotechnical aspects. Description and characterization of glacial materials regarding the proposed environmental and construction activity are typically compiled for evaluation. An example data sheet (Fig. 1) illustrates the range of information obtained (after Skempton et al. 1991). British units (feet) are designated in this paper because those are the units normally used in the data gathering process.

GLACIAL ENVIRONMENTS AND DEPOSITS

Glacial environments yield some of the most complex sedimentary deposits on Earth. Sedimentation occurs in three different environments: beneath the ice as subglacial, atop the ice or supraglacial, or in front of the ice margin as proglacial. The processes of subglacial deposition are the most poorly known as they are inaccessible to direct observation. Deposits formed by supraglacial processes are better known, but more complex, because sedimentation occurs on an unstable substrate (ice) and superglacial deposits commonly undergo several episodes of reworking or resedimentation prior to final deposition. Consequently, the sedimentary record, although conceptually simple, tends to be complex; and detailed description can be challenging.

Diamicton, a glacial geology term, refers to unsorted or poorly sorted deposits that are massive to crudely stratified and consist of a poorly sorted matrix with large clasts (< 2 mm) dispersed throughout. Although a term not typically used in engineering reports, diamicton, as a concept, helps to illustrate the extreme complexity of glacial stratigraphy. They form in a variety of environments—glacial (till, sediment or mudflow deposits, ice-slope colluvium, glacial lacustrine, glacial marine), slopes (colluvium, sediment flow) and volcanic (lahars, volcanic mudflows). Regarding glacial environments, most tills are diam-

1. Location: _____
2. Project: _____ Core file number: _____
3. Submitted by: _____
4. Type samples: _____ Elevation: _____

Sample No.	Sample Depth	Unit Description	Graphic Log	Engineering Data					
				N BPF	Qu TSF	W %	LL %	PI %	Density (wet)

Grain Size				X-ray Data, Mineral Content						
Gvl %	Sd %	St %	Cl %	DI %	M %	I %	C-K %	Cal %	Dol %	Vermiculite Index

Figure 1.—Data form for soil samples, Illinois State Geological Survey.

ictons; but, as indicated above, not all diamictons have a glacial origin.

Till is sediment aggregated by and deposited directly from glacial ice without subsequent disaggregation and resedimentation. A diagram of the ice-margin environment is shown in Fig. 2 (modified from Edwards 1986); the text by Eyles (1983) describes the complex nature of glacial successions.

Till can be subdivided into subglacial (basal) till and supraglacial till. Lodgement and deformation till are found only in the subglacial environment, but melt-out till accumulates in both the subglacial and supraglacial zones. Further consideration yields the following: lodgement till, deposited from or beneath active ice; melt-out till, from inactive or stagnant ice; and deformation till, involving a deforming layer beneath active ice. Melt-out till is sometimes referred to as ablation till.

Lodgement till is massive, poorly sorted, dense and relatively uniform in texture and composition. Sorted sediments, although not common, may occur in thin and irregular bodies or in isolated channel fills. Elongated pebbles in the till show a strong alignment parallel to the direction of ice flow. Subglacial melt-out till is less uniform than lodgement till, contains layers as well as stringers of silt and sand, and has more channel fills; some may have convex upper surfaces, suggesting a tunnel filling.

Supraglacial, melt-out till is less dense and may contain more sorted sediment than the subglacial variety. Because of the dynamic nature of its environment, supraglacial melt-out till is less likely preserved than are other till varieties. Deformation till is essentially lodgement till that has undergone squeezing and shearing.

In addition to till, there are four other major types of glacial deposits: a) sediment flow deposits and ice-slope colluvium, 2) outwash or glacial fluvial deposits, 3) glaciolacustrine deposits, and 4) glacioeolian deposits.

Sediment flow deposits and ice-slope colluvium are glacial features formed by mass wasting in a supraglacial environment. They are formed by plastic to viscous, to semi-fluvial flow of sediment/water mixtures. They are also known as flow tills, and typically are diamictons varying from a few centimeters to

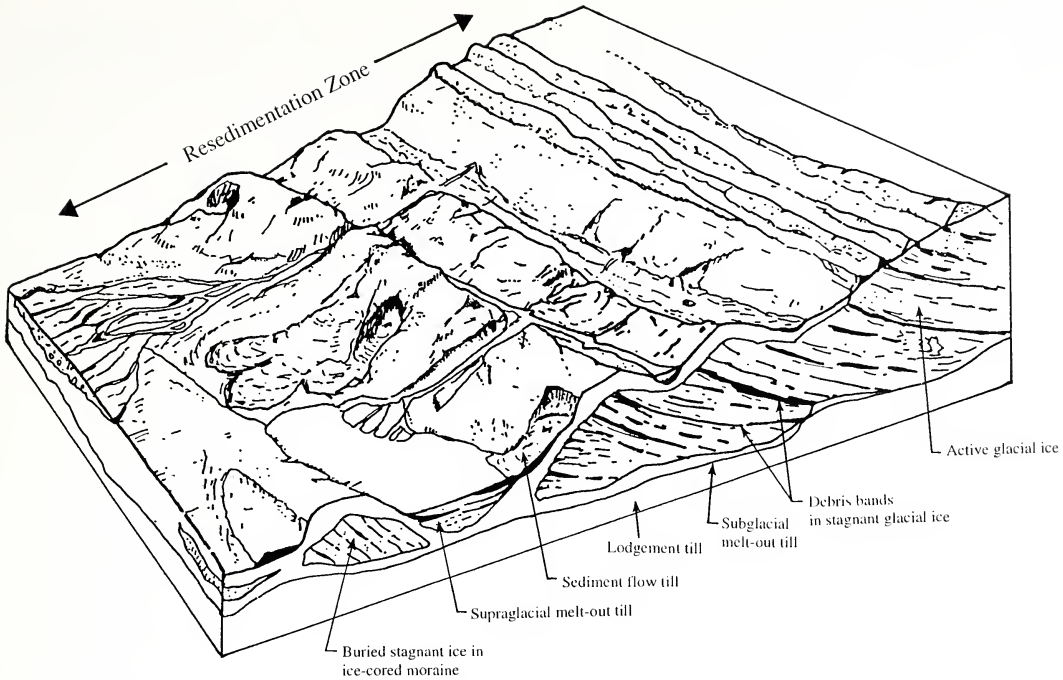

Figure 2.—Schematic diagram of supraglacial/ice-marginal environment. Lodgement till is deposited beneath the active ice; proglacial sedimentation occurs in left portion of the diagram, shows stacking of debris-rich basal ice and concentration of debris by ablation in supraglacial portion. The ice-marginal zone changes continuously during downwasting of the glacier, yielding resedimentation of the debris. (Modified from Edwards 1986.)

a few meters in thickness. In small exposures, without the appearance of flow features, flow till commonly cannot be distinguished from basal till.

Outwash is sediment deposited from meltwater derived from glacial ice. These are fluvial deposits formed by glacial melt water and commonly consist of sand and gravel that is stratified and crossbedded. Deposits generally become finer in the down-flow direction. Sediment flow deposits (flow tills that are diamictons) are commonly interspersed within the outwash.

Glaciolacustrine deposits are formed in lakes in the glacial environments. Lacustrine deposits are generally sorted, stratified and most are fine grained consisting of silt or clay and occasionally sand. Glacioeolian deposits are deposited by wind in the proglacial or periglacial environment. They are either bedload deposits (dune sand, sheet sand) or suspended load (loess) of wind systems that were effective in moving sediment. Loess, which is dominantly silt and usually massive, is deposited downwind of major glacial meltwater streams (see West 1995, Chapter 17, p. 397ff).

GEOTECHNICAL ASPECTS

For engineering geology/geotechnical studies of the Midwest, the drift-covered regions comprise a major portion of the land surface. A simplified designation for the extent of continental glaciation in the eastern United States is as follows: the area north of a line from New York City across Pennsylvania to Pittsburgh, down the Ohio River to the Mississippi River, up river to St. Louis, and then along the Missouri River across the Great Plains into Montana. This boundary is not precise, as there are portions of southern Ohio, Indiana and Illinois that were not glaciated. However, it is a useful estimate of the southern extent of glacial advance. For a map view of this area see West 1995, Chapter 12, p. 254.

Of primary interest for site characterization in the glacial domain are: 1) landform type, 2) type of unlithified material (till, river alluvium, outwash, etc.), and 3) engineering prop-

erties related to the planned construction project. Subsurface investigations regarding building foundations and sanitary landfill siting in a glaciated domain are considered below.

As with all site characterization, description of subsurface conditions is the first order of business. Obtaining background information is the initial step, followed by field reconnaissance, and then a drilling, sampling and laboratory testing program.

The common procedure for subsurface geotechnical investigations in the Midwest in glacial terrain involves HSA (hollow stem auger) drilling and split spoon sampling, using the SPT (Standard Penetration Test). This procedure provides N-values, a measure of density or stiffness of a soil, in blows per foot using the Standard Penetration Test. The split spoon sampler (SS) receives the soil sample, and when retrieved from the subsurface, provides a geologic description and soil samples for subsequent testing.

Some laboratory tests require an "undisturbed" sample to perform the needed testing. Standard penetration test samples cannot be used to perform these tests. Instead, a pushed Shelby tube (ST) is used to obtain samples for these laboratory procedures. Using Shelby tube samples, tests for density, hydraulic conductivity, unconfined compression strength and consolidation are obtained.

Many of the standard engineering tests can also be performed on split spoon samples. These include natural moisture content, Atterberg limits, grain size analysis, specific gravity of solids, and cation exchange capacity (CEC). This same list can be performed on pushed Shelby tube samples.

Tippecanoe County, Indiana.—A proposed landfill site in Tippecanoe County was located in an area of a broad, gently rolling ground moraine (Tipton Till Plain). The site was eight miles (13 km) south of Lafayette's center-city, at the intersection of US-231 and County Road 800 South. Fourteen, 30-foot (9.1 m) deep borings were obtained on this site. The log for Boring A is provided as Fig. 3. Note that the N-value for sample 3 equals 17, but for sample 7 it equals 47. Both 3 and 7 appear to be diamictons, but the high N-value for sample 7 indicates it is likely lodgment till. Sample 3 represents a flow till or ablation till.

Laboratory test results from the Tippecanoe County site are provided in Table 1. Shelby tube samples rather than split spoon samples were used for testing. Silts and clays are represented, but sand units are not included. Note the high dry densities, ranging from 109.5–133.4 lbs/ft^3 and the low moisture contents, ranging from 9.2–16.5%.

These high density, low moisture contents indicate a very dense, high strength soil that has been densified by the weight of the overriding ice. Such materials are designated as overconsolidated because the vertical stress at present is significantly less than it was when a great thickness of glacial ice existed above it. This is also consistent with the low values for the hydraulic conductivity, typically in the 10^{-6} and 10^{-7} cm/sec range. Note also that the cation exchange capacity values (CEC) are below 10 meq/100 grams of dry soil, which are fairly low for clayey soils. Also the plasticity index (PI) values are quite low (1.9–5.0) except for Borings F, M-6 and N-8. A low PI is consistent with low CEC values, both indicating a low clay mineral content.

Indianapolis (Marion County), Indiana.—Subsurface exploration, involving a foundation design for a large building, was conducted on the south side of Indianapolis in an industrial area within the White River floodplain. Although located in the Tipton Till Plain province, the White River floodplain was modified by late stage glacial outwash. One of the boring logs for the site is presented in Fig. 4, where drilling extended into the bedrock.

An upper sand layer (outwash) from 8.5–29 feet, a stiff, silty clay (till) from 29–38 feet and a lower sand layer (outwash) from 38–43 feet are indicated. Seven borings intercepting bedrock, averaging about 50 feet deep, were drilled using HSA and split spoon sampling. The blow counts for the stiff silty clay ranged from 29–57 with an arithmetic mean of 46 (Table 2). Eleven samples of natural moisture content were obtained for the stiff silty clay, yielding a range from 8.8–11.7%, with an arithmetic mean of 9.8%. Dense, overconsolidated till units are indicated by high blow counts (30 or greater) and low (about 10%) natural moisture contents. This is also indicative of a lodgement till.

The Southside Sanitary Landfill, on Kentucky Avenue is located in an area adjacent to

Project Name: Proposed Landfill Date of Boring: November 11, 1981 Boring: A
Drilling Method: HSA
File: Southwest corner-SR 231 & CR 800 South Project No.: ____ Sampling: AU, SS and ST
Tippecanoe County

Description	Depth	Sample	N	Q_u	Q_p	w_c	Remarks
-------Surface----------		1-AU	-	-	-	25	
Dark brown clayey silt to silty clay, trace organic mat.							
Brown silty clay, trace sand	5	2-SS	8	-	-	18	Water level, 6 ft. @ 24HR
Brown silty fine to medium sand	10	3-SS	17	3.3	4.0	10	
Gray silty clay to clayey silt, little sand, trace small gravel		4-ST					Taken 11'6" to 14'6"
	15	5-SS	21	-	-	16	
Gray brown fine to coarse sand, trace small gravel	20	6-SS	50/5"	10	4.5+	8	
Gray clayey silt, some sand, Trace gravel (Till)	25	7-SS	47	7.0	4.5+	8	
	30	8-SS	50/5"	6.5	4.5+	7	

End of Boring

w_c = Natural moisture content
AU = Auger
ST = Shelby Tube
SS = Split Spoon Sample from SPT
SPT = Standard Penetration Test, N values

Figure 3.—Boring log, subsurface exploration, for a proposed landfill in Tippecanoe County. The site was located in an area of a broad, gently-rolling ground moraine.

the boring site described in Fig. 4. It began operations in 1971 and through a series of expansions now occupies over 200 acres (81 ha). However, it lacks a natural clay barrier below the solid waste. Subsurface geology similar to that indicated in Fig. 4 shows the presence of upper and lower sandy units with a silty clay layer between them. To prevent lateral movement of leachate within the upper sand unit, a slurry wall, cut-off trench through the upper unit into the silty clay layer, was proposed. However, the continuity of this silty clay layer throughout the site was questioned based on research by Sudar (1987). If this intermediate clay unit was flow till rather than basal till, it likely would be discontinuous across the site. Therefore, at certain locations, the upper and lower sand units might be directly connected. Field studies were conducted in gravel pit excavations near by, and evidence of both lodgement and flow till units was found. Consequently, field studies could not establish the existence of a continuous till section within the sandy outwash.

The Indiana Department of Environmental Management (IDEM) also concluded that the existence of a continuous layer of silty clay beneath the site had not been proven. Hence, they required that the slurry wall extend through the lower sand unit into the New Albany Shale bedrock. Consistent with IDEM's decision, Sudar (1987) used borings, cross sections, piezometric data and investigation of adjacent active gravel pits to conclude that a high likelihood exists that the silty clay layer is not continuous across the 200 acre (81 ha) site.

Chicago, Illinois.—(The Loop area). The Chicago River and Lake Michigan site are in the Loop area of downtown Chicago, Illinois on a portion of the Calumet Lacustrine Plain where a high-rise building was to be con-

Table 1.—Test results, Tippecanoe County study. * Falling head method, ST = Shelby Tube. CEC results: A, 15′, 6.9 meq/100 g; D, 20′, 8.3 meq/100 g, Avg. = 7.6 meq/100 g.

Boring, Sample, Depth	Visual classification	Dry density (lbs./ft.^{3})	Natural moisture (%)	Atterberg limits: Liquid limit	Atterberg limits: Plastic limit	Atterberg limits: Plasticity index	Hydraulic conductivity* (cm/sec)
A, 4-ST, 11.5–14.5′	Gray silty clay to clayey silt, little sand, trace gravel	128.9	11.8	18.4	13.4	5.0	1.75×10^{-7}
B, 4-ST, 15′–16′4″	Gray sandy clayey silt, little gravel	122.2	14.3	18.9	14.2	4.7	2.43×10^{-6}
C, 4-ST, 12′–13′6″	Gray brown sandy clayey silt, little gravel	127.9	9.2				
E, 6-ST, 18′–20′	Gray clayey silt, some sand, little gravel	133.4	10.3				
F, 3-ST, 10′–12′9″	Brown clayey silt, little sand and gravel	109.5	16.5	38.4	22.9	15.5	
G, 5-ST, 20′–21′2″	Gray clayey silt, some sand, trace gravel	127.5	8.5				
H, 5-ST, 20′–21′2″	Gray clayey silt, some sand, trace gravel	131.1	8.7				
I, 5-ST, 20′–22′9″	Gray silty clay to clayey silt, little sand and gravel	130.8	10.3	17.3	13.4	2.9	1.55×10^{-7}
J, 4-ST, 15′–15′10″	Gray clayey silt, some sand, little gravel		13.5	16.7	13.2	4.5	1.01×10^{-7}
M, 4-ST, 12′–13′8″	Gray clayey silt, some sand, trace gravel	122.2	10.2	15.1	13.2	1.9	7.62×10^{-7}
M, 6-ST, 17′–18′8″	Gray clayey silt, some sand, trace gravel	128.2	10.8	20.6	13.1	7.5	2.64×10^{-7}
N, 6-ST, 17′–18′4″	Gray clayey silt, some sand, little gravel	125.1	11.8	17.9	14.4	3.5	4.9×10^{-5}
N, 8-ST, 25′–26′	Gray clayey silt, some sand, little gravel	121.4	11.4	21.0	12.7	8.3	1.45×10^{-5}

structed. Two borings, drilled 155 and 120 feet (47.2 and 36.6 m) deep, intercepted a 15 foot sand layer, with a soft, silty clay and a stiff, silty clay below. A summary of laboratory test results is provided in Table 3. Soft lacustrine deposits extend from 23.5 to between 48–50 feet deep. Natural moisture contents for these softer soils range from 16.2–24.6% (arithmetic mean = 21.4%). A plasticity index of 19 or 20 was indicated. From 48.5–120 feet the natural moisture content ranged from 8.8–22.2 (arithmetic mean = 15.1%) and the plasticity index ranged from 5–18 (arithmetic mean = 10.2%). The unit extending from 53.5 to 115 or 120 feet is an overconsolidated, basal or lodgement till. Evaluation of N-values for the two borings indicated that three distinct silty clay layers can be discerned: lacustrine from 23.5–50 feet, stiff glacial till from 50–80 feet and a hard glacial till from about 80–120 feet.

Boring logs reveal that the subsurface consists of a surface sand layer (likely beach or dune sand) to a depth of 23 feet with a silty bed (lacustrine) below that to a depth of about 50 feet and an extremely dense silty clay (lodgement till) below, extending to a depth of 120 feet. N-values and natural moisture contents were the primary engineering data used to delineate these contrasting glacial deposits. High-rise buildings in Chicago are founded today on the overconsolidated, basal till or on bedrock.

Elkhart County, Indiana.—(Steuben Morainal Lake Section). The Earthmover's Solid Waste facility, south of the city of Elkhart (Elkhart County, Indiana), is located six miles (3.7 km) northeast of Wakarusa and eight

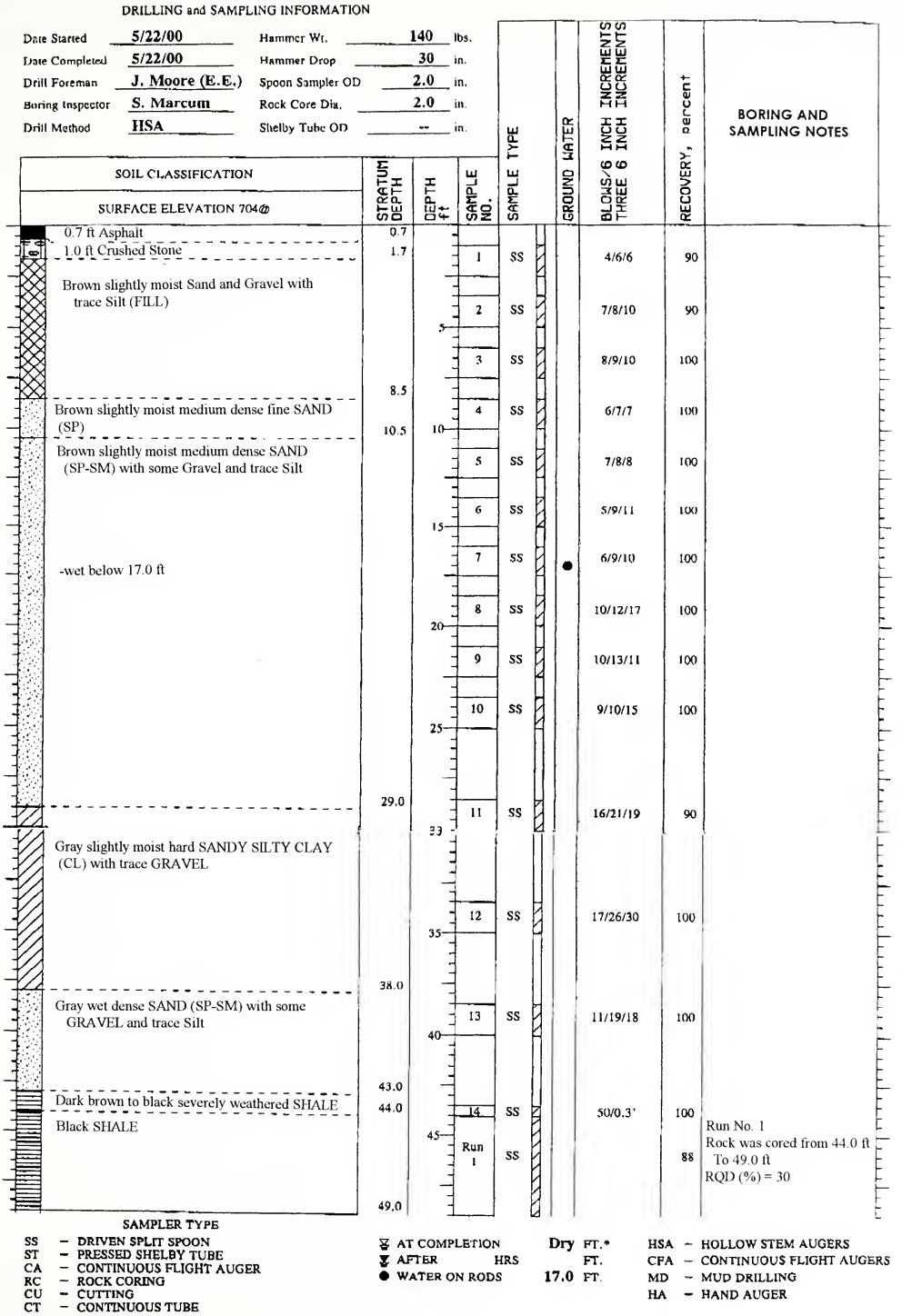

Figure 4.—Indianapolis Project, showing a boring log for the site. The subsurface exploration, involving a foundation design for a large building, was conducted within the White River floodplain.

Table 2.—Natural moisture contents and N values, stiff, silty clay samples, Indianapolis, Indiana. Tsf = tons per square foot, N value = number of blows to drive sample one foot.

Boring No.	Depth (ft)	Natural moisture content, %	Unconfined compression strength (Tsf)	N value (blows/ft)
1	28.5–30.0	11.7		40
	33.5–35.0	10.8		56
2	33.5–35.0	8.9		53
3	33.5–35.0	10.4		45
4	38.5–40.0	10.0		40
5	28.5–30.0	8.8		29
	33.5–35.0	9.6	7.91	47
6	33.5–35.0	9.7		57
	38.5–40.0	9.3		47
7	33.5–35.0	9.5		32
	38.5–40.0	9.4		53

miles (12.8 km) northwest of Goshen. It involves a 45-acre (18.2 hectare) expansion near a complex geologic boundary within the Maxinkukee Moraine. The site is part of the Steuben Morainal Lake Section, with intersecting deposits of the Lake Michigan Lobe from the north and the Huron-Erie (Saginaw) Lobe, from the northeast. For this boundary area, with its complicated glacial stratigraphy, the subsurface is best characterized using the megasequence procedure proposed by Bleuer & Melhorn (1989).

Earthmover's facility, displaying Wisconsin age till at the surface, was only a few miles southeast of the St. Joseph Aquifer System (Reussow & Rohne 1975; DNR 1987), a major regional outwash aquifer, which had to be protected from contamination. Bleuer & Melhorn (1989) proposed that the uppermost unit at the facility is the Post Wakarusa Fan Complex and below it lies the Wakarusa megasequence, consisting of a Wisconsin age till and kame-fan sequence. Underlying are pre-Wisconsin deposits, the Nappanee-Bremen megasequence. Interpretations were made using gamma-ray logs conducted in existing water wells. Details of the Wakarusa megasequence depict an upper clay-rich blocky till with a coarse sandy interval below. The Nappanee-Bremen megasequence consists of clay-rich tills and a clay-free (clean) coarse sand interval.

The clay-free coarse interval within the Nappanee-Bremen megasequence apparently corresponds to the Nappanee aquifer discussed by DNR (1987). The coarse sand intervals (Bleuer & Melhorn 1989) typically occur between elevations 750–780 feet (229–247 m), MSL, with the base of the landfill ranging from 794–811 feet (242–274 m). Bedrock below the site is the green-to-black Ellsworth Shale (Reussow & Rohne 1975), Devonian to Mississippian age. Based on regional data, the depth to bedrock ranges from 200–250 feet (61–76 m) and the ground surface elevation, prior to landfilling, ranged from 806–820 feet (245–250 m).

An idealized gamma ray log and stratigraphic section for the site are provided in Fig. 5. Shown chronologically are the Post-Wakarusa Fan Complex, Wakarusa Megasequence and Nappanee-Bremen Megasequence. Gamma ray logging responds to the clay content because of the increase in radiation typically occurring in clay minerals.

The Post-Wakarusa fan complex, prevalent in the north central portion of the landfill extends offsite to the north. According to test borings it exists from the ground surface (typically about 810 feet) to an elevation of about 796 feet. Sands in the unit are fairly clean, but gamma ray response (Fig. 5) suggests a significant presence of silt and clay. The deposit is interpreted as a pro-glacial fan complex with a typical braided stream pattern. Because of its relatively small extent, the fan complex likely was deposited by a small, lingering lobe of melting ice during final glacial retreat. Initially, meltwater eroded the underlying Wakarusa megasequence; and, as melting progressed, the cut was backfilled with these fan deposits.

Table 3.—Laboratory test results and N values for silty, clay samples, Chicago, Illinois.

Boring No.	Depth (ft)	Natural moisture content, %	Atterberg limits			N value (blows/ft)
			LL	PL	PI	
1	23.5–25.0	18.0				12
	28.5–30.0	16.2				5
	33.5–35.0	19.7				11
	38.5–40.0	21.3				8
	43.5–45.0	22.3	39	19	20	8
	48.5–50.0	19.4				24
	53.5–55.0	19.1				18
	58.5–60.0	19.6	35	17	18	34
	63.5–65.0	19.6				38
	68.5–70.0	17.6				23
	73.5–75.0	18.4	27	16	11	52
	78.5–80.0	16.1				41
	83.5–85.0	16.0				>121
	88.5–90.0	14.7	28	16	12	65
	93.5–95.0	8.8				>124
	98.5–100.0	11.0	21	16	5	>110
	103.5–105.0	11.4		NP		>120
	108.5–110.0	9.5				>200
	113.5–115.0	9.3				>200
2	23.5–25.0	23.0				2
	28.5–30.0	23.5				7
	33.5–35.0	20.3				12
	38.5–40.0	23.3				9
	43.5–45.0	24.6	37	18	19	8
	48.5–50.0	23.0				10
	58.5–60.0	17.1	32	18	14	22
	63.5–65.0	16.3				25
	68.5–70.0	15.2	28	17	11	40
	73.5–75.0	12.8				35
	78.5–80.0	11.8				60
	83.5–85.0	12.5				>100
	88.5–90.0	18.7				>100
	93.5–95.0	12.1				>100
	98.5–100.0	22.2	19	13	6	>100
	103.5–105.0	14.0				>100
	108.5–110.0	11.7				>100
	113.5–115.0	10.8	19	14	5	>100
	118.5–120.0	20.8	39	19	10	>100

A laboratory hydraulic conductivity of 2.3 $\times 10^{-5}$ cm/sec was obtained at the base of this fan, at elevation 798 feet (243 m). This is too permeable to provide a suitable barrier below the waste, and a 10-foot thick, recompacted clay, base liner was required where this unit occurred. This silty material, was suitable, however, for daily cover of trash during landfilling. Hydraulic conductivities for soils samples taken below the landfill base are given in Table 4. Boring WB-25 intercepted the Post-Wakarusa fan complex.

Underlying this fan complex is the Wakausa Megasequence (Fig. 5), typically consisting of a till overlying a coarser sequence of silty and clayey sand. Till below the base of the facility (at 810 feet) is gray to blue-gray, homogeneous silty clay. Percentage of fines (silt and clay combined) typically ranges between 50–90%. Blow counts varied from 20–70 per foot, suggesting that the unit is supraglacial rather than subglacial (or lodgement), which in this area sustains blow counts exceeding 100 per foot. Clay and silt facies of the Wak-

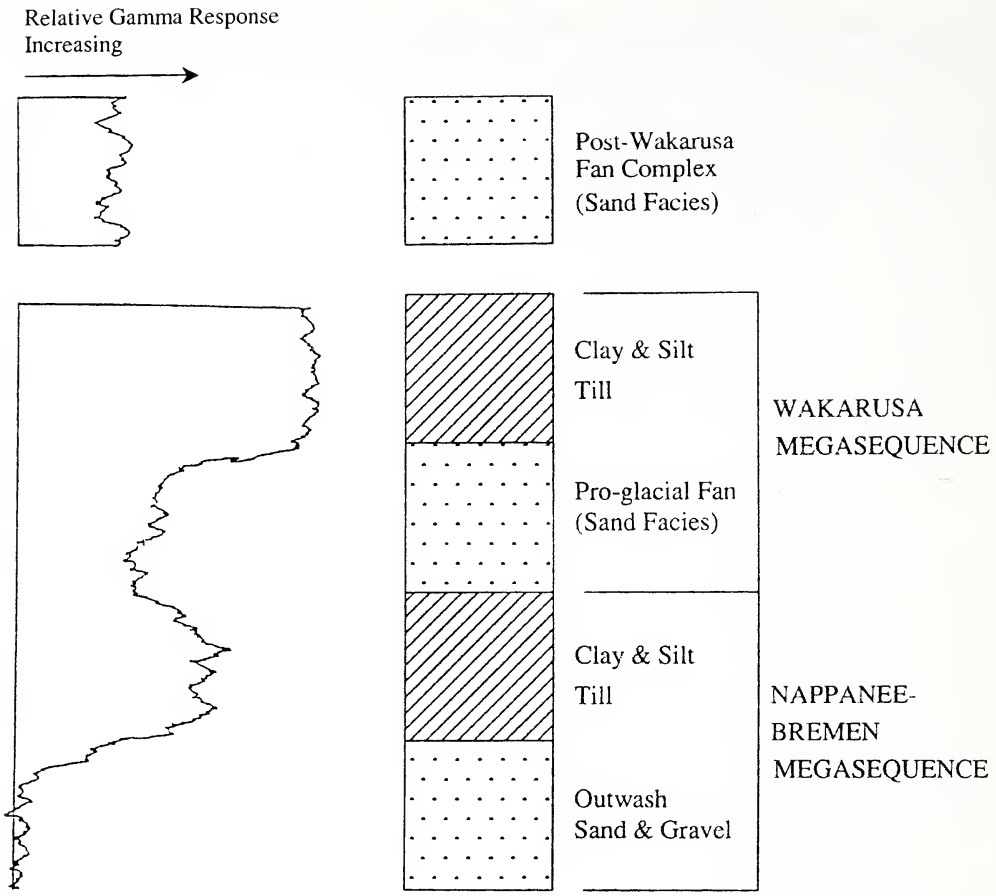

Figure 5.—Idealized gamma Log and Stratigraphic Section, Earthmover's Site, Elkhart, Indiana.

arusa Megasequence are extensive throughout the site, absent only where the Post-Wakarusa Fan complex occurs and the Wakarusa was eroded away. The base of the till unit was found between 770–789 feet elevation. Laboratory hydraulic conductivity values for this zone (Table 4) ranged from 3×10^{-8} to 1×10^{-6} cm/sec (geometric mean = 8×10^{-8}; arithmetic mean = 1.4×10^{-7}). In Table 4 the last entry, 2.3×10^{-5} cm/sec, as indicated above, pertains to the Post-Wakarusa Fan Complex.

The Wakarusa sand facies, a discontinuous silty, clayey, sand body, lies beneath the Wakarusa clay and silt facies. It represents a melt-out feature of Wisconsin glaciation and is probably a fan complex much like the Post-Wakarusa Fan Complex described above. However, it is more widespread. The top of the Wakarusa sand ranges in elevation between 778–804 feet, whereas the bottom elevation ranges from 775–783 feet. Since it is unsuitable barrier material for preventing leachate migration, where the sand occurs less than 10 feet below the bottom of the base grade, a 10-foot recompacted clay liner was added.

The Nappanee-Bremen Megasequence differs from the Wakarusa Megasequence in two major ways: 1) based on its gamma ray signature (Fig. 5) and on borings, it is more variable and not as well defined, and 2) the sand sequences are much cleaner than the Wakarusa sand. The clayey and silty facies of this megasequence have less clay and more silt than the Wakarusa till, but still show low hydraulic conductivities, from 8×10^{-8} to 2×10^{-7} cm/sec. The sand facies are generally continuous from about elevations 775–730 feet, on the eastern half of the site.

Groundwater maps for the Nappanee aquifer at the Earthmover's facility were obtained

Table 4.—Earthmover's Facility, Elkhart County, Indiana. Hydraulic conductivity (k) and Cation exchange capacity (CEC) tests. Tests taken below landfill base. * In-situ test. # = Sample gotten by redrilling B-19 to the specified elevation and obtaining a Shelby tube. B = Early borings, WB = Wehran Company borings.

Boring	Ground elev (ft)	Landfill base elev (ft)	Test elev (ft)	Depth below landfill base, (ft)	k (cm/sec)	CEC Meq/100 g
B-14	817	808	798	10	4.7×10^{-8}	
B-14	817	808	798	10	3.3×10^{-8}	13.9
B-15	817	809	798	11		13.2
B-17	807	794	791	3	3.3×10^{-8}	
B-17	807	794	790	4		20.8
B-17a*	807	794	791	3	2.0×10^{-7}	
B-18	806	798	795	3		15.2
B-19	806	800	795	5		16.8
B-19b#	806	800	794	6	10.0×10^{-6}	
WB-6	808	800	785	15		12.9
WB-9	813	802	792	10	7.5×10^{-8}	
WB-9	813	802	792	10		16.0
WB-10	808	798	793	5	2.0×10^{-7}	
WB-10	808	798	792	6		16.7
WB-11	812	804	791	13		15.2
WB-22	804	798	789	9	3.5×10^{-8}	
WB-23	806	803	796	7	5.1×10^{-8}	
WB-24	819	811	805	6	6.9×10^{-8}	
WB-25	820	808	798	10	2.3×10^{-5}	

on a monthly basis. The Wakarusa sand was unsaturated, and groundwater piezometer data from other units were used to find horizontal and vertical gradients. Groundwater pressure in sand units below the landfill base was a concern. If uplift pressures exceed the downward stress of the overlying soil, a soil pop-up can occur, yielding a spring-like feature in the base of the excavation.

Cation exchange capacity (CEC) data for the site (Table 4) ranged from 12.9–20.8 meq/100g of dry soil, with an average of 15.6. These values are relatively high for clayey soils in Indiana. Recall, for the clayey silt samples in the Tippecanoe County study (Table 1) the CEC values averaged 7.6 meq/100g, which, by contrast, is below average for cohesive, Indiana soils.

Using the megasequence procedure of Bleuer & Melhorn (1989) to develop geologic detail, Wehran Engineering was able to depict the complicated stratigraphy of the site to the satisfaction of IDEM. The landfill extension was designed based on this geologic interpretation, and landfill expansion was accomplished. As indicated above, a 10 foot (3 m) thick, recompacted clay liner was added in areas where sandy zones were found immediately below the landfill base.

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LITERATURE CITED

Bleuer, N. & W. Melhorn. 1989. Glacial Terrain Models, North-central Indiana–The Application of Downhole Logging to Analysis of Glacial Vertical Sequences, Geological Society of Amer-

ica, North-Central Section, Field Trip 2, South Bend, Indiana, April.

Department of Natural Resources. 1987. State of Indiana, Water Resources Availability in St. Joseph River Basin, Indiana.

Edwards, M.B. 1986. Glacial Environments, Sedimentary Environment and Facies (H.G. Reading, ed.). Pp. 45–471.

Eyles, N. 1983. Glacial Geology, An Introduction for Engineers and Earth Scientists. Pergamon Press. 409 pp.

Reussow, J.P. & P.B. Rohne. 1975. Water Resources of the St. Joseph River Basin in Indiana. Hydrolic Investigation Atlas, HA-0537. U.S. Geological Survey, Reston, Virginia.

Skempton, J.P., R.C. Berg & D.R. Soller. 1991. Glacial Geology of the Midwest. Framework and Applications, Short Course, 34th Annual meeting, Association of Engineering Geologists, Chicago, Illinois.

Sudar, Susan A. 1987. Subsurface and Hydrogeologic Investigation of the Existing Operations and Proposed Expansion of South Side Sanitary Landfill, Marion County, Indiana. M.S. Thesis, Purdue University. 148 pp.

Wehran Engineering Corporation. 1989. Permit Amendments for Solid Waste Disposal Facility, Expansion for Earthmover's Incorporated, Elkhart, Indiana.

West, T.R. 1995. Geology Applied to Engineering, Prentice-Hall. 560 pp.

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THE RELATIONSHIP BETWEEN GLACIAL GEOLOGIC PROCESSES AND PEATLAND DISTRIBUTION IN INDIANA

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ABSTRACT. Peat-filled depressions are not randomly distributed in Indiana. The higher frequency of kettles and peatlands in northern Indiana is attributed to the dynamic processes of glacial retreat rather than potential influences of pre-glacial topography. Ninety percent of Indiana's peatlands occur in the northern moraine and lake region of the state. Within this region, peatlands were significantly more frequent inside the former boundaries of the Saginaw Lobe than peatlands occurring outside of this area. An analysis of peatland distribution and specific glacial drift types in Noble County showed that peatlands were significantly more frequent in mixed till and stratified drift in lineated form associated with collapse of sub-ice tunnels and open ice-walled channels. Four other drift types contained significantly fewer peatlands than expected.

Keywords: Bog, fen, glacial geology, Indiana, kettle, lake, peatland, wetland

Although peat deposits occur in many places around the world, the northern latitudes of the former Soviet republics, Canada, and the United States have the largest coverage (Lucas 1982). The abundance of peatlands in these northern regions is the result of poor drainage, limited water circulation, and cool, humid climates on a local or regional scale. Where the regional climate is characterized by cool humid summers, long winters, and abundant even rainfall, peatlands may form relatively unbroken expanses that blanket flat or gently rolling topography. But in areas with less favorable climates, such as the Midwest interior of the United States, the distribution of peatlands is usually dictated by microclimates provided by isolated geographic features.

While recognizing the importance of regional climate in peatland initiation, Taylor (1907) states that the glacial topographic features of Wisconsinan Age are a greater factor than climate in the geographic position of the peat deposits of the Midwest. Because peatlands in lower Michigan, Indiana, and other midwestern states are restricted to these isolated glacigenic depressions, their distribution can be attributed to specific glacial and fluvioglacial processes. Most investigators associate the formation of these peat-filled depressions with the melting of isolated blocks of buried glacial ice. Some have hypothesized that the formation of ice-block depressions was favored by pre-glacial valleys that slowed the melting of ice and became receptacles for outwash from surrounding uplands, thus increasing the chances for ice to become buried (Flint 1971). Andreas (1985) proposed that pre-glacial valleys may have facilitated the formation of kettles in Ohio and consequently determined the distribution of the associated peatlands. The objectives of the present study are to determine the present and historic distribution of Indiana peatlands and investigate the potential influence of specific glacial events and pre-glacial topography on peatland distribution in Indiana.

STUDY AREA

The study area includes the part of Indiana covered with glacial drift of Wisconsinan age—approximately the northern two-thirds of the State. Evidence for drifts from at least two previous glaciations in Indiana, the "Kansan" (often a collective term for pre-Illinoian drifts) and Illinoian, has been reported (Melhorn 1997). Most of these, with the exception of portions of the Illinoian drift in southern Indiana, have been covered or obliterated by Wisconsinan drifts. The drifts in northern Indiana range from 15–150 m thick (Wayne 1956). The thickest deposits (averaging 90 m thick) occur throughout the interlobate area of the former Saginaw and Erie Lobes in north-

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east Indiana. The drift becomes shallower to the west and south, where it averages 45 m thick. The bedrock underlying this unconsolidated material is composed chiefly of shale—relatively friable sedimentary deposits of Devonian and Mississippian Age (Howe 1997). The lime-rich glacial drift imparts a strongly alkaline reaction on the groundwater and, consequently, that of the lakes and wetlands of the region.

METHODS

Data sources.—Determination of the current and pre-settlement distribution of peatlands in Indiana was obtained from three sources: 1) a list of 68 peatlands registered with the Indiana Natural Heritage Database of the Indiana Department of Natural Resources, Division of Nature Preserves (IDNR-DNP), 2) an inventory of commercial peat deposits (potential and active) in Indiana compiled by Schneider & Moore (1978), and 3) soil surveys of the United States Department of Agriculture (USDA) for all 92 Indiana counties. Each data source was treated separately in the statistical analyses due to the potential differences in the types of peatlands represented in terms of soil classification and vegetation composition and structure.

Mapping.—Peatland distribution was compared to maps of pre-glacial river valleys (Gutschick 1966), late-Wisconsinan glacial coverage (Wayne 1966), and the distribution of Quaternary geologic units (Gray 1989) by digital overlay of the maps. The aerial coverage of the various geologic units used in the statistical analyses was determined cartographically.

Statistical analyses.—Chi-square Goodness of Fit tests comparing peatland frequency and distribution to landscape physiography were conducted by constructing "1 × 2" Chi-square tables ($df = 1$). Expected values were based on a null hypothesis that peatlands would be equally distributed across all physiographic units. After the area of each respective physiographic unit (e.g., Saginaw Lobe, buried river valleys, Quaternary diamicton) was determined, its percent coverage was calculated. The expected frequency for peatlands in each unit was determined by multiplying the percent aerial coverage of each unit by the total number of peatlands in the respective analysis.

The portion of Indiana covered by Wisconsinan glacial deposits was analyzed to determine the relationship between peatland distribution and buried river valleys. Thirty-five percent of that area is underlain by known buried river valleys [based on the map by Gutschick (1966)]. Since it must be assumed that some inaccuracies occur in the mapped locations of pre-glacial river valleys, comparison of the underlying valleys with existing peatlands was based on relative "association." Peatlands which were within, or in contact with, the border of a buried river valley were considered associated.

Another analysis of peatland frequency was restricted to the Northern Moraine and Lake Region (Mallott 1922) to study the influence of the Saginaw Lobe. The expected distribution of peatlands for the Chi-square test was based on the estimated aerial coverage of the former Saginaw Lobe which was determined to be 36% of the Northern Moraine and Lake Region.

A spatial analysis of the most characteristic peatland soil, Houghton Muck, was conducted for Noble County, Indiana by combining information from the 53 soil maps for the county and comparing the distribution of peatlands and other wetlands to Quaternary geologic units (Gray 1989). A digital map overlay and subsequent Chi-square analysis was then conducted.

RESULTS AND DISCUSSION

Peatland frequency & distribution in Indiana.—Sixty-two peatlands (90%) registered in the IDNR-DNP Natural Heritage Database (Fig. 1, Table 1) occurred in the Northern Moraine and Lake Region of Indiana. No peatlands occurred south of the Wisconsinan glacial boundary. Schneider & Moore (1978) report 265 commercial quality peat deposits in Indiana. All are restricted to the area north of the Wisconsinan glacial boundary (Fig. 2). Two hundred and forty-one (91%) occur in the Northern Moraine and Lake Region, and 24 (9%) occur within the Tipton Till Plain (Fig. 2). These percentages are similar to those discussed above for registered peatlands.

The concentration of Indiana peatlands, as well as other wetlands and lakes, in the Northern Moraine and Lake Region is not simply a function of the presence of glacial deposits. Glacial deposits cover most of Indiana. Some

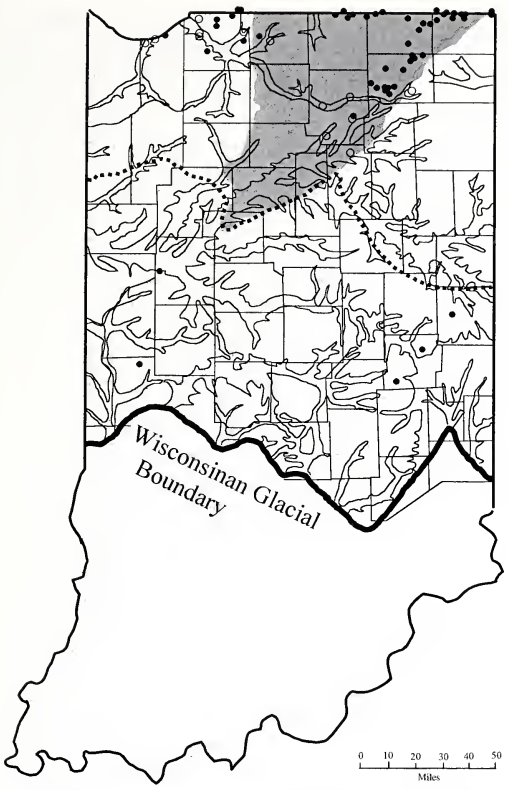

Figure 1.—Map of Indiana showing 1) extent of Wisconsinan glacial deposits (thick, solid line), 2) margin of the Northern Moraine and Lake Region (dotted line), 3) extent of the former Saginaw Lobe circa 15,000 ybp (shaded area), the distribution of buried river valleys as determined by Gutschick (1966), and 4) the distribution of 68 peatlands registered with the Indiana Division of Nature Preserves. A solid dot (●) is a peatland not associated with a known pre-glacial valley, and an open dot (○) is a peatland situated over or extremely close to a known pre-glacial valley.

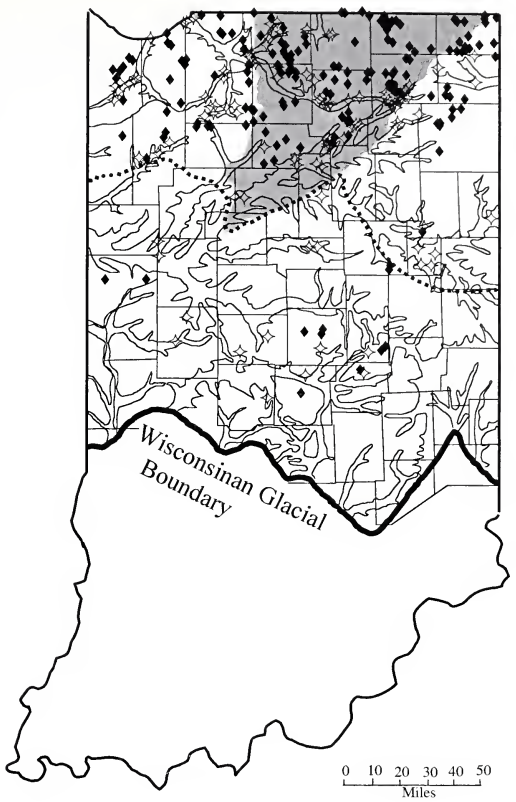

Figure 2.—Map of Indiana showing 1) extent of Wisconsinan glacial deposits (thick, solid line), 2) margin of the Northern Moraine and Lake Region (dotted line), 3) extent of the former Saginaw Lobe circa 15,000 ybp (shaded area), the distribution of buried river valleys as determined by Gutschick (1966), and 4) the distribution of 265 commercial quality peat deposits (from Schneider & Moore (1978)). A solid diamond (♦) is a peat deposit not associated with a known pre-glacial valley, and an open diamond (◇) is a peat deposit situated over or extremely close to a known pre-glacial valley.

other factor or factors must be responsible for the creation of kettles and other depressions favorable to peat formation.

Indiana peatland distribution and buried river valleys.—Andreas (1985) proposed that Ohio peatland distribution is related to pre-glacial (buried) river valleys. Andreas's study is the only known study in our region that is concerned with the relationships between peatland distribution and glacial and pre-glacial landforms. She referenced previous theories that ice masses remained frozen longer in pre-glacial valleys, and that this condition facilitated kettles and other depressions favorable to peatland development.

The distribution of peatlands in Indiana was compared to the location of pre-glacial valleys (Figs. 1, 2). Although the 68 registered peatlands considered in the present study seem to reflect the overall distributional pattern of peat in Indiana (Fig. 1), they probably do not represent an independent sample. The fact that these peatlands are extant and protected may be because some factors hindered their drainage for agriculture and other development. Therefore, these peatlands were treated separately from a potentially more independent

Table 1.—Location and physiography of Indiana peatlands registered in the Indiana Division of Nature Preserves Database. *A* = Alluvium; silt, sand and gravel deposits of and along present streams (includes some colluvium along valley margins); *BD* = Beach and dune sand along present and recently abandoned beaches; *LS* = Lake sand, beach sand, and slack-water sand and silt deposits of broad, shallow post-glacial lakes (Includes much washed ablation drift and many small areas of dune sand); *S* = Dune sand; *O* = Undifferentiated outwash, mainly as valley train; sand and gravel Atherton Formation in part; *OF* = Outwash-fan deposits; sand and gravel; *OP* = Intensely pitted outwash deposits, principally in fan form but including also some kame terrace, sand gravel; *TG* = Mixed drift; till and stratified drift in chaotic form; *TT* = Mixed drift, till and stratified drift in lineated form indicating collapse associated with subice tunnels and open ice-walled channels; *TW* = Clay-loam to silt-loam till of Wedron Formation; *MW* = areas of morainal topography (Wedron Formation); *TC* = Silty clay-loam to clay-loam till of Lagro Formation; *TC/M* = Thin clay-loam till over buried morainal topography; *TB* = Loam till of Trafalgar Formation; *MB* = Areas of morainal topography (Trafalgar Formation). An asterisk denotes peatlands associated with buried river valleys.

Peatland	County	Elevation	Drift type	Peatland type
Blueberry Bog	Elkhart	263.6	OP	Basin, Bog
Umbrella Sedge Bog	Elkhart	228.6	OP	Basin, Bog
Bristol Fen	Elkhart	235.6	S	Basin/Riparian, Fen
Elkhart Bog	Elkhart	235.6	O	Basin, Bog
Leatherleaf Shrub-Carr	Elkhart	237.7	S	Basin, Bog
Disko High Bogs	Fulton	268.2	TG	Basin, Fen
New Castle Fen	Henry	310.8	O	Riparian, Fen
Knightstown Fen	Henry	301.7	O	Riparian, Fen
Kiser Lake Fen*	Kosciusko	266.6	OP	Basin, Fen
Backwaters Fen	Kosciusko	259.9	OP	Basin, Fen
Stafford Lake Site	Kosciusko	264.8	TG	Basin, Bog
Little Arethusa Bog*	Kosciusko	264.2	TG	Basin, Bog
Burket Bog*	Kosciusko	249.9	TT	Basin, Bog
Chapman Lake Wetlands*	Kosciusko	252.3	O	Basin, Bog
Springfield Fen Site	La Porte	210.3	O	Basin, Fen
Trail Creek Fen*	La Porte	185.9	O	Riparian, Fen
Mt. Pleasant Bog	La Porte	244.7	MW	Basin, Bog
Autumn Bog	La Porte	265.1	MW	Basin, Bog
Pinhook Bog*	La Porte	249.9	TG	Basin, Bog
Lost Bog*	La Porte	252.9	TG	Basin, Bog
Thompson Bog	La Porte	231.9	MW	Basin, Bog
Fish Creek Fen	La Porte	211.8	OF	Riparian, Fen
Yellow Birch Wetland	La Porte	222.5	MW	Basin, Fen
Shoemaker Bog	La Porte	233.1	OF	Basin, Bog
Mill Creek Fen*	La Porte	220.9	OF	Basin, Fen
Olin Lake Site	Lagrange	274.3	TG	Basin, Fen
Cline Lake Fen	Lagrange	280.4	TB	Basin, Fen
Shipshewana Fen	Lagrange	249.9	S	Riparian, Fen
Fawn River Fen	Lagrange	262.1	S	Riparian, Fen
Yost Pond	Lagrange	252.9	OP	Basin, Bog
Tamarack Bog Site	Lagrange	277.3	O	Riparian, Fen
Martin Fen	Lagrange	280.4	O	Riparian, Fen
Lane Lake Fen	Lagrange	268.2	O	Basin, Fen
Mounds Fen*	Madison	256	O	Riparian, Fen
Long Swamp Woods	Noble	275.8	TT	Basin, Bog
Leatherleaf Bog	Noble	285.3	TC	Basin, Bog
Indian Village Bog	Noble	274.3	OF	Basin, Bog
Christlieb Bog*	Noble	286.5	TC/M	Basin, Bog
Bush Cinquefoil Site	Noble	285.0	TC/M	Basin, Fen
Dutch Street Bog	Noble	289.6	O	Basin, Bog
Cletus Stump Bog	Noble	271.3	OP	Basin, Bog
Hickory Bog	Noble	289.6	TC	Basin, Bog

Table 1.—Continued.

Peatland	County	Elevation	Drift type	Peatland type
Svoboda Fen	Noble	289.6	TB	Basin, Fen
Tamarack Bog	Noble	274.3	TC	Basin, Bog
Eagle Lake Wetlands	Noble	267.0	O	Basin, Fen
Sylvan Lake Site	Noble	279.2	O	Basin, Fen
Wolf Lake Site	Noble	274.3	TT	Basin, Fen
Clock Creek Site	Noble	270.1	O	Riparian, Fen
Turkey Run Site	Parke	155.5	A	Riparian, Fen
Portage Fen*	Porter	185.9	BD	Riparian, Fen
Cowles Bog	Porter	182.9	BD	Basin/Riparian, Fen
Garyton Wetland*	Porter	189.0	LS	Basin, Fen
Cabin Creek Raised Bog	Randolph	320.0	TB	Riparian, Fen
Kankakee Fen Site	St. Joseph	218.8	O	Basin, Fen
New-Oak-Road Bog*	St. Joseph	251.5	TW	Basin, Fen
Ropchan Memorial Bog	Steuben	292.6	TG	Basin, Bog
Handy Lake Site	Steuben	316.7	TC/M	Basin, Fen
Seven Sisters Site	Steuben	298.7	TG	Basin, Bog
Nevada Mills Bog	Steuben	298.7	TB	Basin, Fen
Beaverdam Lake	Steuben	284.4	OP	Basin, Fen
Beechwood Site	Steuben	317.0	O	Basin, Fen
Tamarack Lake Site	Steuben	289.3	TG	Riparian, Fen
Steuben County Notable #37A	Steuben	294.1	TG	Basin, Bog
Marsh Lake Wetlands	Steuben	294.7	TG	Basin, Fen
Binkley Fen	Steuben	295.7	MB	Basin, Fen
Lime Lake Site	Steuben	286.5	OP	Basin, Fen
Big Swamp	Steuben	317.0	O	Basin, Fen
Flint Creek Fen	Tippecanoe	161.5	O	Riparian, Fen
Laketon Bog*	Wabash	225.6	O	Basin/Riparian, Fen

source provided by Schneider & Moore (1978) for commercial peat. A Chi-square Goodness of Fit Test of the relationship between buried valleys and registered peatland distribution in Wisconsinan deposits indicated that registered peatlands are not significantly more frequent over buried valleys (Table 2). Similarly, analysis of Schneider & Moore's (1978) commercial peat data shows that these deposits are not significantly more frequent over buried river valleys within the Wisconsinan glaciated region of Indiana (Table 3).

If pre-glacial valleys facilitated the formation of post-glacial depressions, then it would be expected that central Indiana, being underlain by the most distinct and numerous pre-glacial valleys, would harbor as many peatlands as other areas of the state; but it does not. The peatlands that are disjunct—those occurring near the southernmost boundary of the Wisconsinan glaciation—were probably formed in the depressions in the more uneven topography resulting from development of relatively significant moraines. The latter is un-

Table 2.—Chi-square table showing that the frequency of peatlands registered with the Indiana Division of Nature Preserves, is not significantly greater over river valleys buried by Wisconsin-age deposits ($df = 1$; $\alpha = 0.001$).

Location in Wisconsin-age deposits	Observed (f)	Expected (f_c)	$f - f_c$	$(f - f_c)^2$	$(f - f_c)^2/f_c$
Buried river valleys	14	23.8	−9.8	96.04	4.04
Other areas	54	44.2	9.8	96.04	2.17
Total	68	68	0		6.21

Table 3.—Chi-square table showing that the frequency of commercial quality peat deposits (Schneider & Moore 1978), is not significantly greater over river valleys buried by Wisconsin-age deposits ($df = 1$; $\alpha = 0.001$).

Location in Wisconsin-age deposits	Observed (f)	Expected (f_c)	$f - f_c$	$(f - f_c)^2$	$(f - f_c)^2/f_c$
Buried river valleys	105	92.75	12.25	150.06	1.62
Other areas	160	172.25	−12.25	150.06	0.87
Total	265	265	0		2.49

common in central Indiana; and hence, peatlands are uncommon there.

For pre-glacial depressions to influence post-glacial features, they would have to endure three glacial advances: the Kansan (pre-Illinoian), Illinoian, and the Wisconsinan. The ability of relatively minor pre-glacial depressions to affect post-Wisconsinan topography, in Indiana at least, is questionable. These pre-glacial valleys would have long ago been filled with glacial debris. Groundwater flow in these thick glacial deposits might result in subsidence caused by dissolution of some till constituents, which could create depressions suitable for peatland formation. This, however, is probably insignificant and does not explain the scarcity of peatlands and other wetlands in central Indiana where buried river valleys abound.

Regional glacial processes.—Indiana peatland distribution, indicative of kettles and other glacial depressions, seems more related to glacial processes. Inspection of Gutschick's (1966), Wayne's (1966), and Gray's (1989) maps, with comparison to Indiana peatland distribution, seems to illustrate a greater relationship with specific glacial features and processes than pre-glacial topography.

The association of peat, peatlands, and their kettle, kame, and esker complexes to the Saginaw Lobe of the Laurentide Ice Sheet (approximately 15,000 ybp) is pronounced. Within the Northern Moraine and Lake Region, commercial quality peatlands [as determined by Schneider & Moore (1978)] were significantly more frequent within the former boundaries of the Saginaw Lobe (Fig. 2, Table 4), than peatlands occurring outside of this area. Peatlands registered with the Indiana Division of Nature Preserves were also significantly more frequent within the Saginaw Lobe region (Fig. 1, Table 5).

Although several histosols are referred to as peat, the most characteristic peatland soil is Houghton Muck. Houghton Muck is generally restricted to the northern third of the state and constitutes 149,009 acres (62,087 ha) for the State (see Swinehart 1997). Counties with the greatest coverage of Houghton Muck are in northeast and north-central Indiana. These counties are all found within the region formerly occupied by the Saginaw Lobe (Figs. 1, 2) and comprise 41.3% of the total coverage of Houghton Muck in Indiana. This is further evidence of the role of the Saginaw Lobe in

Table 4.—Chi-square table showing that the frequency of commercial quality peat deposits (Schneider & Moore 1978), is significantly greater within the area formerly occupied by the Saginaw Lobe, than other areas within the Northern Moraine and Lake Region in Indiana ($df = 1$; $\alpha = 0.001$).

Location in northern moraine and lake region of Indiana	Observed (f)	Expected (f_c)	$f - f_c$	$(f - f_c)^2$	$(f - f_c)^2/f_c$
Saginaw Lobe	130	83.52	46.48	2160.39	25.87
Other Lobes	102	148.48	−46.48	2160.39	14.55
Total	232	232	0		40.42

Table 5.—Chi-square table showing that the frequency of peatlands registered with the Indiana Department of Natural Resources, Division of Nature Preserves, is significantly greater within the area formerly occupied by the Saginaw Lobe, than other areas within the Northern Moraine and Lake Region in Indiana ($df = 1$; $\alpha = 0.001$).

Location in northern moraine and lake region of Indiana	Observed (f)	Expected (f_c)	$f - f_c$	$(f - f_c)^2$	$(f - f_c)^2/f_c$
Saginaw Lobe	46	22.32	23.68	560.74	25.12
Other Lobes	16	39.68	−23.68	560.74	14.13
Total	62	62	0		39.25

creating depressions suitable for peat formation.

The importance of the Saginaw Lobe to kettle and peatland formation is due to its unique manner of deterioration. Unlike the adjacent Erie and Michigan Lobes which receded actively (ablation simply exceeded accumulation), the Saginaw Lobe was apparently cut off by outwash channels on all sides (Wayne 1966). This resulted in stagnation and downmelting (Bleuer 1974). The importance of these processes in the Saginaw Lobe region is supported by the presence of mixed stratified drift in chaotic form and the lack of uniform ground and end moraines (Gray 1989). As the Saginaw Lobe deteriorated, it likely became highly fragmented, and large blocks of ice were separated from the main mass of ice. Superglacial sediment, which accumulates on the marginal zone of a glacier during down-melting (Clayton & Moran 1974), probably buried isolated blocks of ice. The presence of the Lake Michigan and Erie Lobes on either side of the Saginaw Lobe created large outwash channels for the flow of meltwater, further contributing to the burial of isolated ice-blocks. This burial insulates the ice and facilitates kettle formation. The abundance of classic kettle depressions around the periphery of the former Saginaw Lobe is evidence of these interlobate processes.

Local glacial processes and Quaternary geologic units.—Registered peatland distribution was compared to post-glacial topography. Sixty-eight percent of the peatlands are associated with interlobate moraines, primarily the Packerton and Valparaiso, the former harboring the greater percentage. The remaining peatlands in the Northern Moraine and Lake Region are otherwise distributed about the margins of the former Saginaw Lobe. Six registered peatlands occur within the southern portions of the Tipton Till Plain.

Comparing registered peatland distribution to specific glacial landforms as determined by Gray (1989) showed 44% (30) occurring in outwash deposits, 23% (16) occurring in till, 21% (14) occurring in mixed drift (till and outwash), and 12% (8) occurring in sand, lacustrine, or alluvial deposits (Table 1). Peatland elevations ranged from 155.5–320.0 m with a mean of 262.4 m (SD = 35.7). The elevation of Indiana peatlands seems to be relatively consistent within the 215–275 m levels. No significant associations were noted between peatland distribution and regional elevation.

To gain further insight into the factors contributing to peatland formation, a more detailed spatial analysis was conducted on the wetlands of Noble County. Noble County was chosen because it intersects the interlobate area in northeast Indiana, contains the greatest percent coverage of peat of any Indiana county, and represents a great diversity of glacial drift-types. Classification of the kettles was based on the contents of the basins: those occupied by Houghton Muck (peatlands), those occupied by emergent vegetation and/or humified histosols, and those containing open water (lakes). The spatial analysis was based on occurrence only, and not size, of the respective wetlands. Peatlands, other wetlands, and lakes were found throughout the county except for the extreme northwest corner (Fig. 3).

The observed frequency and distribution of peatlands in the various drift-types across the

Table 6.—Glacial drift types and associated peatlands, other wetlands, and lakes in Noble County, Indiana. Drift type follows Gray (1989): *TC/M* = Thin clay-loam till over buried morainal topography; *O* = Undifferentiated outwash, mainly as valley train; sand and gravel Atherton Formation in part.; *MB* = Areas of morainal topography; *TB* = Loam till of Trafalgar Formation; *TC* = Silty clay-loam to clay-loam till of Lagro Formation; *TT* = Mixed drift; till and stratified drift in lineated form indicating collapse associated with subice tunnels and open ice-walled channels; *OP* = Intensely pitted outwash deposits, principally in fan form but including also some kame terrace. Sand gravel; *TG* = Mixed drift; till and stratified drift in chaotic form; *OF* = Outwash-fan deposits; sand and gravel; *G* = Ice-contact stratified drift, sand and gravel as isolated ridges; *MC* = Areas of morainal topography of Lagro Formation; *LS* = Lake sand, beach sand, and slack-water sand and silt deposits of broad, shallow post-glacial lakes. Includes much washed ablation drift and many small areas of dune sand; *TS* = Loam to silty clay loam till. A "+" indicates that the lake or wetland is significantly more frequent than expected probability, and a "−" indicates that the lake or wetland is significantly less frequent than expected probability ($df = 1$; $\alpha = 0.05$).

Drift type*	% area	Area (ha)	Observed (f) peatland	Expected (f_e) peatland	χ^2 Value peatland	Observed (f) wetland	Expected (f_e) wetland	χ^2 Value wetland	Observed (f) lakes	Expected (f_e) lakes	χ^2 Value lakes
TC/M	35	36833.36	303	296.22	0.24	56 (−)	90.18	19.83	40	42.66	0.20
O	14	14895.36	135	119.79	2.25	62 (+)	36.47	20.79	19	17.25	0.21
MB	13	13637.96	85 (−)	109.68	6.37	22 (−)	33.39	4.46	15	15.80	0.05
TB	10	10234.51	57 (−)	82.31	8.61	11 (−)	25.06	8.73	2 (−)	11.85	9.06
TC	7	7647.17	66	61.50	0.59	21	18.72	0.30	6	8.86	0.99
TT	7	6939.88	107 (+)	55.81	50.23	34 (+)	16.99	18.21	25 (+)	8.04	38.29
OP	6	6021.01	38	48.42	2.37	29 (+)	14.74	14.62	12	6.97	3.84
TG	5	4908.70	50	39.48	2.95	19 (+)	12.02	4.26	1 (−)	5.69	4.05
OF	3	2732.43	3 (−)	21.97	16.81	3	6.69	2.09	2	3.16	0.44
G	2	1946.55	6 (−)	15.65	6.06	3	4.77	0.66	1	2.25	0.71
MC	<1	229.72	3	1.85	0.72	0	0.56	0.56	0	0.27	0.27
LS	<1	132.99	1	1.07	0.00	0	0.33	0.33	0	0.15	0.15
TS	<1	30.23	0	0.24	0.24	0	0.07	0.07	0	0.04	0.04
Total	100	106189	854	854		260	260		123	123	

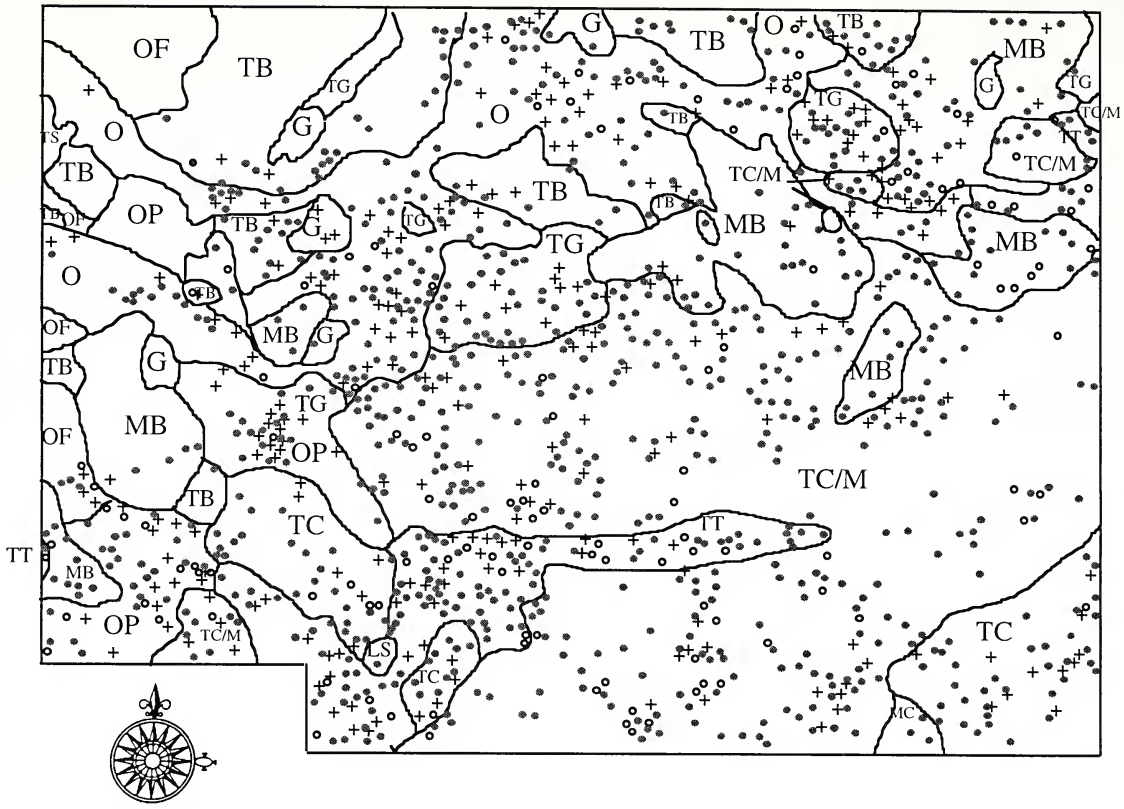

Figure 3.—Map of Noble County, Indiana, showing the location of peat deposits (●), marshes and humified histosols (○), and lakes (+) in relation to glacial drift types. *TC/M* = thin clay-loam till over buried morainal topography; *O* = undifferentiated outwash, mainly as valley train; sand and gravel of Atherton Formation in part; *MB* = areas of morainal topography; *TB* = loam till of Trafalgar Formation; *TC* = silty clay-loam to clay-loam till of Lagro Formation; *TT* = mixed drift; till and stratified drift in lineated form indicating collapse associated with subice tunnels and open ice-walled channels; *OP* = intensely pitted outwash deposits, principally in fan form but including also some kame terrace; sand and gravel; *TG* = mixed drift; till and stratified drift in chaotic form; *OF* = outwash fan deposits; sand and gravel; *G* = ice-contact stratified drift, sand and gravel as isolated ridges; *MC* = areas of morainal topography of Lagro Formation; *LS* = lake sand, beach sand, and slack-water sand and silt deposits of broad, shallow post glacial lakes; includes much washed ablation drift and many small areas of dune sand; *TS* = loam to silty clay-loam till. (Drift types after Gray (1989).

county was similar to expected values, with the exception of *MB* (areas of morainal topography of Trafalgar Formation), *TB* (loam till of Trafalgar Formation), *OF* (outwash fan deposits; sand and gravel), *G* (ice-contact stratified drift, sand and gravel as isolated ridges), and *TT* (mixed till and stratified drift in lineated form associated with collapse of sub-ice tunnels and open ice-walled channels) (Fig. 3, Table 6). *MB*, *TB*, *OF*, and *G* contained significantly fewer peatlands than expected, while *TT* contained significantly more peatlands than expected (Table 6). The dearth of peatlands in some drift-types might be explained by considering the local glacial and fluvio-glacial processes. Both *MB* and *TB* are tills of the Trafalgar formation, mostly resulting from moraines. While ice-blocks can occur in moraines, it seems less likely due to the active manner in which they are created. However, some aspect of the moraines of Lagro Formation, perhaps their high clay content, location over slightly older Wisconsinan tills, and proximity to the interlobe, favored the formation of more numerous peat-filled depressions than moraines of Trafalgar origin.

Reduced frequency of peatlands in *G* is probably due to the relatively high elevation of the ridges and the porous nature of the drift (mainly sand and gravel). The scarcity of peatlands in *OF* is curious, because sediment laden meltwater would likely facilitate the formation of water-filled depressions. The reduced number of peatlands in this drift-type may be primarily a function of proximity to the glacier margins rather than local processes, although, few of the registered peatlands across the state were associated with *OF* (Table 1).

Nearly twice as many peatlands and wetlands, and more than three times as many lakes, occurred in *TT* than random distribution would yield. These statistics suggest that processes associated with ice deterioration and stagnation strongly facilitate the formation of kettles and other depressions. *TT* results from collapse of a large ice tunnel within older drift overlain by till of the Lagro Formation (Gray 1989). The lakes in Chain o' Lakes State Park are an excellent example of the result of this kind of formation process.

The distribution and frequency of peatlands differs substantially from other wetlands. While both peatlands and wetlands were significantly more frequent in *TT*, wetlands additionally were unusually abundant in *O* (undifferentiated outwash, mainly as valley train; sand and gravel), *OP* (intensely pitted outwash), and *TG* (mixed till and stratified drift in chaotic form). All of these areas are likely to be characterized by relatively low elevations, highly permeable materials, and good drainage. Areas such as *TC/M* (thin clay-loam till over buried morainal topography), *MB*, and *TC*, where wetlands were few, contain finer constituents, are less permeable, and probably more conducive to peat rather than muck formation.

CONCLUSIONS

The factors affecting the formation and distribution of peatlands in the southern Great Lakes region are hierarchical. At the coarsest level, glacial processes, such as the stagnation of entire lobes of ice, facilitated the formation of kettles. The local processes that determined the texture and composition of the drift affected drainage and, consequently, the limnology and ontogeny of resulting lakes and wetlands.

It is concluded that peat-filled depressions are not randomly distributed in Indiana. High kettle and peatland frequency in northern Indiana is attributed to the dynamic processes of glacial retreat in that area. Although it has been speculated that buried valleys are responsible for the creation of environments favorable to peatland formation in Ohio, this study proposes that most peatlands in Indiana, regardless of underlying topography, are a direct result of the downmelting of the Saginaw Lobe of the Laurentide ice-sheet and other aspects of dynamic deterioration of glacial ice. These conclusions suggest that microclimates provided by glacial topography may be a more important factor in the distribution of peatlands in temperate regions than regional climate.

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LITERATURE CITED

Andreas, B.K. 1985. The relationship between Ohio peatland distribution and buried river valleys. Ohio Journal of Science 85:116–125.

Bleuer, N.K. 1974. Geologic story of Pokagon State Park. Dept. of Natural Resources, Indiana Geological Survey, Bloomington. 4 pp.

Clayton, L. & S.R. Moran. 1974. A glacial process-form model. *In* Glacial Geomorphology. (D.R. Coates, ed.). Publications in Geomorphology, State University of New York, Binghamton. 398 pp.

Flint, R.F. 1971. Glacial and Quaternary Geology. John Wiley & Sons, New York. 892 pp.

Gray, H.H. 1989. Quaternary geologic map of Indiana. Dept. of Natural Resources, Indiana Geological Survey, Bloomington.

Gutschick, R.C. 1966. Bedrock geology In Natural Features of Indiana. (A.A. Lindsey, ed.). Indiana Academy of Science, Indianapolis. 600 pp.

Howe, R.C. 1997. Of time, rocks, and ancient life: Bedrock geology. Pp. 3–13, *In* The Natural Heritage of Indiana (M.T. Jackson, ed.), Indiana University Press. Bloomington, Indiana.

Lucas, R.E. 1982. Organic soils (histosols) B Formation, distribution, physical and chemical properties, and management for crop production. Michigan State University Agricultural Experiment Station and Cooperative Extension Service, Research Report 435 Farm Science. 77 pp.

Mallott, C.A. 1922. Physiography of Indiana. *In* Handbook of Indiana Geology. (W.N. Logan, ed.). Indiana Department of Conservation, Publication No. 21, Pt. 2, Pp. 59–256.

Melhorn, W.N. 1997. Indiana on ice: The late Tertiary and ice age history of Indiana Landscapes. Pp. 15–27, *In* The Natural Heritage of Indiana (M.T. Jackson, ed.). Indiana University Press. Bloomington, Indiana.

Schneider, A.F. & M.C. Moore. 1978. Peat resources of Indiana. Department of Natural Resources, Indiana Geological Survey, Bulletin 42-0. 32 pp.

Taylor, A.E. 1907. The Peat Deposits of Northern Indiana. Indiana Department of Geology and Natural Resources, 31st Annual Report. Pp. 73–298.

Wayne, W.J. 1956. Map showing thickness of drift in Indiana north of Wisconsinan glacial boundary. Indiana Department of Conservation, Report of Progress 7, Plate 1.

Wayne, W.J. 1966. Ice and land: A review of the Tertiary and Pleistocene history of Indiana. *In* Natural Features of Indiana. (A.A. Lindsey, ed.). Indiana Academy of Science, Indianapolis. 600 pp.

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THE POTENTIAL ROLE OF LAKE BASIN MORPHOMETRY IN THE FORMATION AND DEVELOPMENT OF PEATLANDS IN INDIANA

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ABSTRACT. Numerical support for generalizations about factors favoring peat formation in kettles is scant. Kettle morphometry was examined on the basis of fetch orientation, shoreline development, surface area, maximum depth, mean depth, and relative depth. The only significant feature separating peat-forming kettles from non-peat-forming kettles was surface area. Small basins seemed most likely to become peat-forming due to reduced wind and wave-induced erosion. Protected shores were more likely to develop a floating mat that favored the genesis and build-up of peat. The chemistry and ecology of the successive stands of vegetation that eventually colonized the peat was most affected by watershed area and hardpan permeability (which ultimately determined the degree of minerotrophy).

Keywords: Bog, fen, glacial geology, Indiana, kettle, lake, morphometry, peatland, wetland

Although most of the peatlands in the southern Great Lakes region are associated with glacial kettle depressions, an equal or greater number of such depressions never develop into peatlands. This indicates that some basin-specific factor or factors must determine whether or not a particular lake or pond will develop into a peatland rather than a more common marsh, swamp, or slough.

Many investigators have considered the effects of basin morphometry on the ontogeny and senescence of lakes. Taylor (1907) suggests that *small* glacial lakes and ponds were the most favorable geographic features for peat formation due to reduced wave action. Similarly, Gates (1942) states that bogs [in the sense of *Sphagnum*-dominated peatlands] may develop in any open-water depression (shallow or deep) or small embayment of a larger waterbody that is small enough to prevent significant wave action. Both Taylor and Gates view wave action as destructive to the marginal mat of vegetation and thus, a hinderance to the establishment of peat-forming plant communities. Although Crum (1988) also recognizes the negative impact of wave action in the stability of peat-forming marginal mats, he points out that wave action also positively influences the magnitude of seasonal overturn (and thus nutrient cycling) in a basin, which may reduce the likelihood of peat formation.

Crum characterizes "kettlehole" lakes that are commonly occupied by peat as having a small surface area, cold water, and an abrupt drop-off. Transeau (1905) and Davis (1907) also discuss the magnitude of drop-off. Both authors associate the slope of the basin walls with the coverage of littoral vegetation and the dynamics and source of vegetable detritus. However, they do not elaborate on whether steep slopes might favor peat formation as opposed to the formation of more common, humified sediments. While Ruttner (1953) remarks that the development of a floating mat, typical of "quaking bogs," is likely only over shallow benches and in protected bays, Wilcox & Simonin (1988) conclude that classic floating-mat peatlands are largely a function of deep, steep-sided basins that allow horizontal mat growth to exceed vertical peat accumulation.

Although general summaries outlining the proposed importance of basin morphometry on peatland formation have been presented, no known comparisons between the morphometry of these depressions and non-peat-forming depressions have ever been made.

The present study examines how certain morphometric qualities of some basins made them predisposed toward peatland development. Northern Indiana was the focus of the

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study because the regional climate and topography are unfavorable for the development of blanket mires, thus restricting peatlands to small, isolated depressions. Because the regional climate is not optimal for extensive peat formation over large areas of the landscape, these Indiana peatlands may facilitate the study of the specific qualities of lake basins that favor peatland formation. The objectives of the study were to examine and characterize the morphometric qualities of peat-filled depressions and compare them to non-peat-filled lake basins.

STUDY AREA

Northeast and north-central Indiana is characterized by hundreds of lakes that stretch from the Huron River Valley of Michigan (see Transeau 1905) through the northeast corner of Indiana to a point nearly 160 km southwest. These lake basins consist of kettle holes, irregularities in moraines, and channel lakes, created in the interlobate region of the former Saginaw and Erie Lobes of Wisconsin age (Scott 1916). The lakes occurring west of the interlobate area (north-central Indiana) are a result of the stagnation and deterioration of the Saginaw Lobe *circa* 15,000 ybp (years before present) (Wayne 1966).

While examples of several types of lake basins have been identified in Indiana by Scott (1916), most would be best classified as kettle lakes. Lakes resulting from the scouring of rock or the damming of pre-glacial valleys are absent in Indiana (Scott 1916). Other types of basins, such as those resulting from irregularities in ground moraine are most common in areas where pre-glacial relief strongly influenced glacial and post-glacial topography and drainage. This situation was probably not present in Indiana at the onset of Wisconsin glaciation, due to the presence of significant, pre-Wisconsin glacial deposits already in place over the bedrock topography. Hutchinson (1975) reports that in the glaciated parts of North America east of the Rocky Mountains, the number of kettle basins is likely far greater than that of all other types of basins considered together.

STUDY SITES

The 10 basins that were selected for detailed morphometric analysis occur mainly in northeast Indiana (Kosciusko, Lagrange, Noble, and Steuben Counties) with the exception of Shoemaker Bog in northwest Indiana (La Porte County). All have developed typical peatland plant communities. Burket, Dutch Street, Leatherleaf, Shoemaker, and Yost Bogs are *Sphagnum*-dominated leatherleaf (*Chamedaphne calyculata*) bogs. Little Chapman and Hickory bogs are *Sphagnum*-dominated, but lack a significant low shrub component. Binkley and Svoboda Fens are non-*Sphagnum*-dominated peatlands with bush-cinquefoil and sedges as dominant vascular plants. Tamarack Bog is a non-*Sphagnum*-dominated peatland with a dense tree canopy dominated by red maple (previously dominated by tamarack).

All of the sites, given their relative depth, are probably kettles. While the large area collectively called Chapman Lake (formerly Little Eagle Lake) may be the result of irregularities in the ground moraine, as proposed by Scott (1916), the associated sub-basin occupied by Little Chapman Bog, due to its depth and shape, is probably of ice-block origin.

Hutchinson (1975) recognizes five types of kettles based on how they were formed: 1) kettles or cavities left by melting of ice-blocks in outwash discharged into a pre-existing valley, 2) kettles in drift-filled valleys, the drainage having no relationship to the pre-existing hydrography, 3) kettles in pitted outwash plains, 4) kettles in till of continental ice sheets, and 5) kettles in eskers. Most of the sites conform to types 3 and 4. Hickory Bog is a classic example of type 5, resulting from linear strips of ice from the lower parts of the side walls of sub-glacial streams becoming embedded in the sides of an esker (Hutchinson 1975), and is probably the first record of this type of kettle in Indiana.

METHODS

Morphometry.—Depth of the basins was determined by systematic soundings with metal rods. Soundings were made at 25 m intervals (arranged in a grid) on small basins ($\leq$ 10 ha) and 50 m intervals on larger basins ($<$ 10 ha). The bottom of the basin was defined as the depth at which sand or gravel was reached; overlaying clays and silts were penetrated by the probe and were included in the total depth. Bathymetric maps were constructed by transferring the data to maps drawn

from aerial photos and connecting equal depth points (see Swinehart 1997).

Definitions for and calculation of fetch (F) (or maximum effective length; the shoreline was defined as the point where the surface of organic wetland sediments interfaced with inorganic glacial drift), maximum breadth (b_m), shoreline length (L), shoreline development (D_L), surface area (A), maximum depth (Z_m), mean depth (Z), volume (V), and relative depth (Z_r) follow Hutchinson (1975). Values for F, b_m, L, and A were determined cartographically.

Stratigraphy.—A modified Hiller-type corer was used to retrieve sediment samples for stratigraphic analysis of six peatlands. A single core was taken from the deepest known point in each peatland. While sediment layers can be unevenly distributed throughout a basin (see Rigg & Richardson 1938), most basins have relatively horizontal layers of sediment (see Rigg & Richardson 1938; Scott & Miner 1936; Wilson 1938), especially kettles lacking distinct sub-basins which may have different sediment accumulation rates. In the present study, it was assumed that the stratigraphy of the various sediment layers was relatively uniform across the basin.

Sediment-type was determined by microscopic analysis. Three major stratigraphic units were identified. Lake sediments were usually highly decomposed (sapric) but contained subfossils of submergent and emergent aquatic macrophytes such as *Ceratophyllum demersum*, *Najas flexilis*, *Potamogeton* spp., *Nymphaea tuberosa*, *Nuphar advena*, and *Brasenia schreberi*. Fen sediments were less humified (hemic) and were dominated by brown moss subfossils, primarily *Drepanocladus aduncus*. *Sphagnum*-peat was composed almost entirely of well-preserved (fibric) remains of *Sphagnum* spp., with lesser amounts of wood and leaves of ericaceous shrubs.

Radiocarbon dating was conducted by Mass Accelerator Spectrometry at the Purdue Rare Isotope Measurement Laboratory.

RESULTS & DISCUSSION

Although the concentration of peat-forming wetlands and non-peat-forming wetlands may vary between different glacial regions and different drift types, peatlands and other wetlands are, more often than not, found in close proximity. So, there must be some more specific qualities of individual basins that favor the development of peatlands over other types of wetlands.

Surface area, fetch, and orientation of the long axis: The surface area of 25 peatlands listed in Table 1 ranged from 0.6–39 ha, with a mean area of about 19 ha (SD = 11.2). The areas of these peatlands are similar to those of peat-filled kettles described by other investigators (Coburn et al. 1932; Rigg & Richardson 1934, 1938; Welch 1936, 1938a, 1939; Karlin & Lynn 1988; Andreas & Bryan 1990). While many investigators observe that peat-filled kettles in the southern Great Lakes region are small, none have presented numerical comparisons with the average area of water-filled kettles as a whole. To support the conclusion that peat-filled kettles are characteristically small, some comparison must be made with non peat-forming kettles.

The surface area of 248 glacial lakes in Indiana (data from Sanderlin 1984), ranged from 0.8–1239 ha with a mean of 59 ha (SD = 114.19). These data suggest that most kettles occupied by peat are much smaller than non-peat-filled kettles in Indiana. Large peatlands, some over several hundred hectares in area, have been reported in the southern Great Lakes region (Andreas & Knoop 1992); but they are extremely rare.

The influence of area, like most morphometric parameters, on peatland formation is limnological in nature and affects the ontogeny of a lake long before it becomes a bog or a fen. The significance of surface area to the biological, chemical, and physical characteristics of lakes has been discussed by many authors (see Welch 1952; Ruttner 1953; Lerman 1978; Cole 1983; Wetzel 1983). Its effects on wind and wave action are of primary consideration because agitation of the water-surface influences shoreline erosion as well as the chemical and thermal characteristics of the water. Given the variation in the chemical and thermal characteristics of both bog-lakes and other types of lakes, it appears that shoreline erosion is the most significant factor in the formation of lake-fill peatlands.

Length and orientation of the fetch also influence the magnitude of shoreline erosion. The longer the uninterrupted distance of open water, the greater is the potential amplitude (and thus erosive force) of waves (Wetzel 1983). The fetch of peat-filled kettles in In-

diana ranged from 115–1370 m (Table 1) with a mean of 615 m (SD = 294.6). Intuitively, the relatively small area of the peatlands will result in a relatively short fetch, unless a particular basin is unusually oblong or linear. While all of the kettles had sparsely developed shorelines (Table 1), most were slightly oblong rather than truly circular. Only four (16%) of the kettles approached the shape of a circle, therefore the orientation of the long axis becomes important in terms of potential wave generation and erosion. Examination of the fetch orientation yielded no consistency among the peat-filled kettles. The importance of fetch orientation may be difficult to ascertain because prevailing winds may have changed throughout the late-Pleistocene and Holocene.

Smaller basins with a short fetch, or with a fetch oriented perpendicular to prevailing winds, are most likely to be sheltered from erosive waves, favoring accumulation of a "false-bottom" of organic material (Welch 1936, 1938a, 1939). Although wind-swept lakes can develop a false bottom due to erosion by waves (Welch 1938b), flocculent sediments rarely accumulate around the margins. The presence of marginal accumulations of flocculent organic material, favored by shelter from wind initiates the formation of a peat-forming mat. This observation is supported by the presence of many kettles with peat mats developed exclusively or primarily on the windward side of the lake rather than on the wave-battered shore (Crum 1988).

When undisturbed organic sediments along the shoreline build up to the point where they approach the water surface, they become a substrate for sedges and mosses. In times of low water, these colonies consolidate, develop a matrix of stems and roots, and become a floating fen mat. With a hinged substrate free from flooding and standing water, horizontal mat growth can far exceed vertical sediment accumulation. What may result is a major change in the ecology of a lake simply because the mat further reduces area, and the area that the mat now occupies is no longer open to free diffusion of oxygen into the water. Consequently, the chemistry and productivity of the oxygen-poor mat, also poor in plant-available macro-nutrients, may deviate drastically from what would be expected based on the chemistry of the open lake water. Reduced contact with groundwater as a result of semi-impermeable organic sediments, along with cation exchange by brown mosses (Glime et al. 1982), and eventually by *Sphagnum*, can form an acid-forming mat on an extremely alkaline lake. Examples of such conditions include Egg Lake, Beaver Island, Michigan (Swinehart 1996a) and Inverness Mud Lake, Cheboygan County, Michigan (Welch 1936). However, even in these lakes, the open water is likely altered because the mat affects the flow of nutrients by catching and holding allochthonous litter and nutrients.

Because small lakes are protected from wind and waves, the magnitude of seasonal overturn may be reduced (Wetzel 1983; Crum 1988). Whether this factor truly favors peatland formation is questionable since most peat production is restricted to the margins of the lake at the interface between air and water. This location would seem to be exempt from any unique thermal/hydrodynamic qualities of the rest of the water volume. Only nutrient availability and primary productivity should be affected by reduced seasonal overturn. Recharge of oxygen to anoxic sediments would be reduced, transport of nutrients from the hypolimnion to the epilimnion would be reduced, and consequently, nutrient availability would be reduced due to permanent incorporation in the sediments of the hypolimnion. While a cold, proportionally large hypolimnion that is subjected to little mixing could accelerate in-filling by limiting reduction of organic detritus during settling, the resulting sediments never approach the fibric character of peat formed at the margins of the lake.

Productivity of a lake, as a whole, need not affect peatland development. Peatlands may form on either eutrophic or oligotrophic lakes as long as local decomposition is significantly less than local productivity. This condition occurs where the mat occupies the air-water interface, thus reducing oxygen saturation, decreasing temperature of the substrate as a result of evapotranspiration, and consequently reducing bacterial decomposition.

Depth: Kettle lakes are not characteristically deep in comparison to other types of lake basins (glacial or otherwise). They are relatively shallow inclusions in the glacial drift, and they vary in maximum depth from less than a meter to over 45 m (see Coburn et al. 1932; Wilson 1938; Scott & Minor 1938;

Table 1.—Morphometric data for 25 peatlands in Indiana: Fetch, maximum breadth (b_m), surface area (A), maximum depth (Z_m), mean depth (Z_{mean}), ratio of mean depth to maximum depth ($Z_{mean}:Z_m$), relative depth (Z_r), volume (V), shoreline length (L), and shoreline development (D_L). * Orientation of the long axis given in parentheses. [1] Smith (1937), [2] Prettyman (1937), [3] Howell (1938), [4] Lindsey (1932), [5] Swickard (1941), [6] Wilcox & Simonin (1988), [7] Richards (1938), [8] Otto (1938), [9] Keller (1943), [10] Hamp (1940) [Data obtained from these sources restricted to depth. All other values were obtained cartographically by the author.]

Peatland	*Fetch (m) & orientation	b_m (m)	A (m^2)	Z_m (m)	Z_{mean} (m)	$Z_{mean}:Z_m$	Z_r (%)	V (m^3)	L (m)	D_L
Little Chapman Bog	305 (circular)	305	90000	15	3.9	0.26	4.43	232710	1100	1.03
Burket Bog	990 (N-S)	395	250000	15	7.2	0.48	2.66	1187050	3050	1.72
Shoemaker Bog	685 (N-S)	610	150000	8	2.9	0.36	1.83	284770	2135	1.55
Yost Bog	380 (NS-SW)	100	80000	12	6.5	0.54	3.76	339890	915	1.0
Dutch Street Bog	685 (N-S)	75	160000	15	6.3	0.42	3.32	669232	2135	1.51
Svoboda Fen	460 (circular)	460	250000	14	6.6	0.47	1.59	1086360	1950	1.10
Leatherleaf Bog	305 (N-S)	230	40000	9	2.3	0.26	3.99	62215	1525	2.15
Tamarack Bog	760 (N-S)	380	140000	10	3.0	0.30	2.37	278200	2135	1.61
Hickory Bog	115 (NE-SW)	65	6000	4.5	3.2	0.72	5.15	12995	365	1.33
Binkley Fen	760 (W-E)	610	310000	10	4.9	0.49	1.59	998995	2315	1.17
Lake Cicott Bog[1]	1800 (W-E)	300	300000	15	—	—	—	—	1525	1.0
Fox Prairie Bog[2]	530 (W-E)	460	220000	12	—	—	—	—	1465	1.0
Kokomo Bog[3]	1370 (NE-SW)	380	300000	10	—	—	—	—	3050	1.57
Little Arethusa Bog	800 (NE-SW)	300	150000	17	—	—	—	—	2440	1.78
Merrillville White Pine Bog[4]	685 (W-E)	460	300000	12	—	—	—	—	2440	1.26
Mill Creek Fen[5]	600 (N-S)	300	170000	18	—	—	—	—	2135	1.46
Mt. Pleasant Bog	760 (NE-SW)	380	180000	12	—	—	—	—	2440	1.62
Pinhook Bog[6]	1140 (NW-SE)	533	380000	18	—	—	—	—	3170	1.45
Thompson Bog	305 (W-E)	230	60000	11	—	—	—	—	915	1.05
Otterbein Bog[7]	700 (circular)	700	380000	10	—	—	—	—	2135	1.0
Bacon's Swamp (bog)[8]	265 (NE-SW)	75	125000	10	—	—	—	—	—	—
Culver Bog[9]	610 (N-S)	380	170000	13	—	—	—	—	1830	1.25
Round Lake Bog[10]	760 (circular)	760	390000	10	—	—	—	—	2440	1.10
Ropchan Memorial Bog	610 (W-E)	425	140000	9	—	—	—	—	1525	1.15
Jeff Bog[9]	265 (NW-SE)	150	40000	16	—	—	—	—	609	1.0

Kratz & DeWitt 1986; Miller & Futyma 1987; Wilcox & Simonin 1988). It is often implied and sometimes explicitly proposed (see Wilcox & Simonin 1988) that kettles most favorable to peatland or floating mat development are "deep." To support such an observation, measurements of peat-filled kettles and non-peat-filled kettles are needed to place the parameter of depth into a relative context.

Maximum depth of peat-forming kettles in Indiana ranged from 4.5–18 m (Table 1) with a mean of 12.2 m (SD = 3.36). Unfortunately, very little data exists on the original depths of non-peat-forming kettle lakes, as only a few have been probed beyond the surface of the sediments (Scott & Miner 1936; Wilson 1938). For general comparison purposes, the maximum water depth (not inclusive of accumulated sediments) of 248 glacial lakes in Indiana was compiled. Maximum depths ranged from 2.4–37 m with a mean of 12.4 m (SD = 6.37). This mean is nearly equivalent to that determined for the peat-forming kettles, even though the total maximum depth of the non-peat-forming kettles was not available. Consequently, it must be assumed that their true maximum depth is much greater. Over 15 m of sediment has been found beneath the water column in some Indiana lakes (Scott & Miner 1936; Wilson 1938). With these points considered, it is very likely that peat-forming kettles are shallower on average than non-peat-forming kettles, at least in terms of maximum depth.

Mean depth, the ratio of mean to maximum depth, and relative depth probably depend mostly on the position of the original ice block in the till and the amount of debris in the ice block. Masses largely exposed at the surface would likely retain much steepness and depth, whereas masses buried with appreciable overburden would likely be shallower and have gradual slopes due to slumping (Fig. 1).

Mean depth of Indiana peatlands ranged from 2.3–7.2 m (Table 1) with a mean of 4.7 m (SD = 1.84). The ratio of mean to maximum depth ranged from 0.26–0.54 with a mean of 0.43 (SD = 0.14). Mean relative depth averaged 3.07% (SD = 1.25), ranging from 1.59–5.15%. Hutchinson (1975, pp. 168–169) summarizes the morphometric parameters from lakes that are especially deep (mainly grabens, calderas, and fjords), and those that have particularly large surface areas (primarily lakes formed from glacial corrasion). These summaries serve as examples of relatively deep and relatively shallow lake basins, respectively. The ratio of mean depth to maximum depth averaged 0.44 in relatively deep lakes and 0.35 in relatively shallow lakes. Relative depth averaged 3.13% in relatively deep lakes and 0.065% in relatively shallow lakes. Comparing these values to the data given in the present study (Table 1) suggests that the kettles examined are "relatively deep" (deep for their size), even though paludification of surrounding upland can create shallow rims causing underestimation of the original relative depth of the lake before infilling.

Whether the relative depth of kettles favorable to the formation of floating mats and peat is greater than that for other kettles is doubtful, even though there is insufficient morphometric data to allow a definitive conclusion. It is likely, however, based on what is known of current hydrography, that if the original morphometry of non-peat-forming kettles was measured, as it was for Winona and Tippecanoe Lakes (Scott & Miner 1936; Wilson 1938), no significant differences in relative depth would be observed. Thus, it seems that the importance of great depth in peat and mat formation is not well supported.

Wilcox & Simonin (1988) suggest that deep basins allow a mat to grow horizontally across the surface without becoming grounded by vertical accumulation of detritus peat. The primary argument against this theory is that horizontal mat growth can far exceed vertical sediment accumulation. Even if the detritus peat in a shallow basin was accumulating at an extremely fast rate of 3 cm per year, a floating mat of leatherleaf (*Chamaedaphne calyculata*) can advance as much as 6.3 cm per year (Swan & Gill 1970) and likely much faster for sedge mats. Another problem is that the theory does not take into account rising water tables during the Holocene (see Miller & Futyma 1987) that would progressively increase distance between the mat and the detritus peat.

While Wilcox & Simonin (1988) conclude that deep, steep-sided basins are most favorable to peat formation, Ruttner (1953) states that development of a floating mat is favored only over shallow benches and in protected bays. It seems clear that such formations can

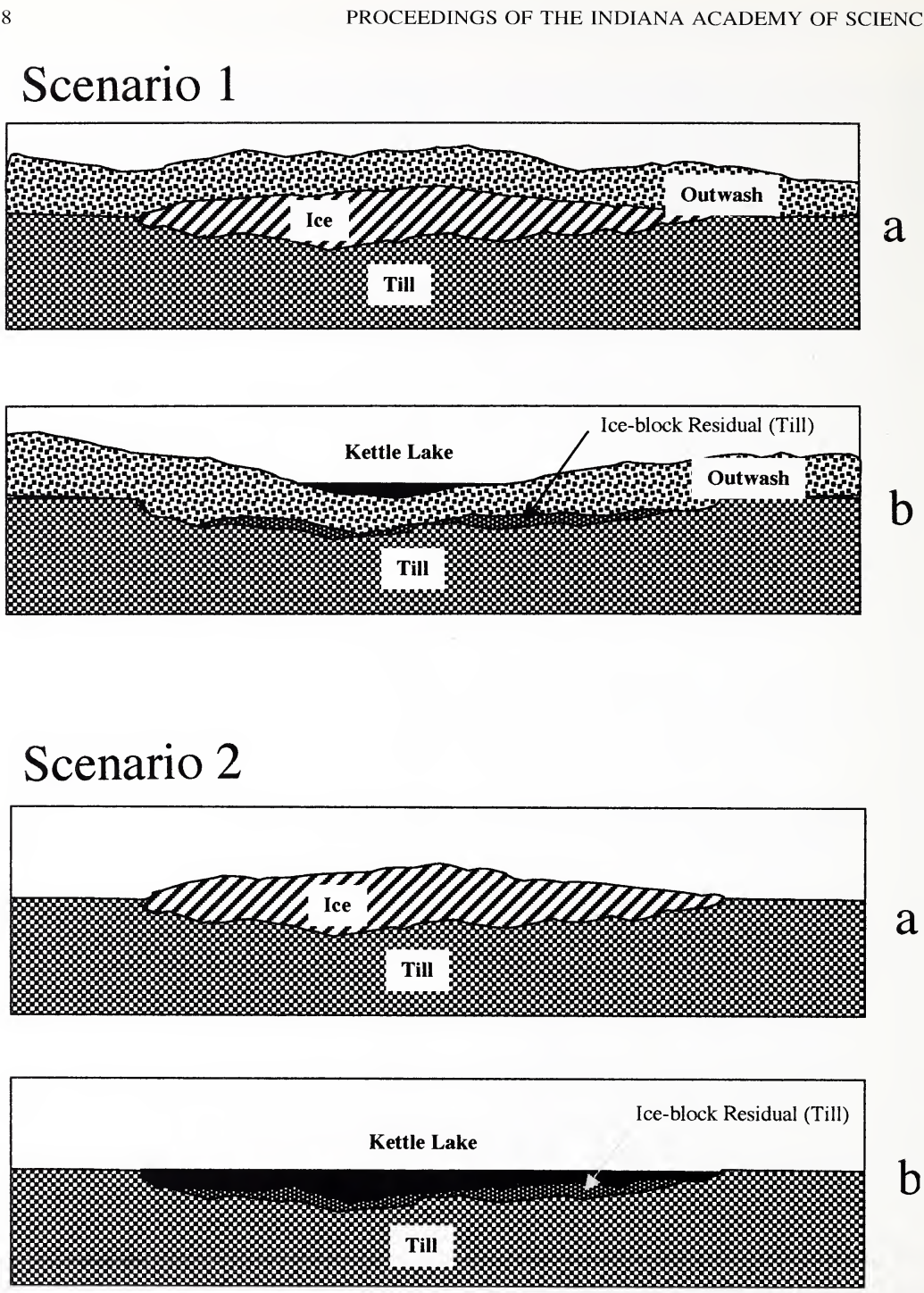

Figure 1.—Conceptual model of kettle lake formation. In Scenario 1 the glacial ice block is covered with overburden (a), and the resulting kettle (b) has gently sloping margins due to slumping. In Scenario 2, the ice block is exposed at the surface (a), and the resulting kettle (b) has steeply sloping margins.

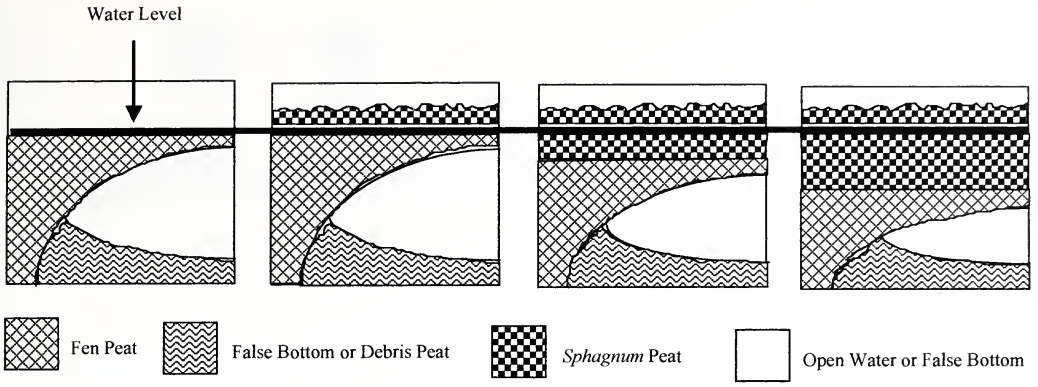

Figure 2.—Conceptual model of the compaction of a floating mat and underlying sediments after successive build-up of peat. Eventually, the mat becomes grounded, compaction is significantly reduced, and decomposition increases significantly at the surface. Note that the interface between *Sphagnum* peat and fen peat that was initially formed at or above the water surface is pushed below the water level over time.

occur over both shallow and deep water. The tendency for floating mats to be found more commonly over deep water is likely due to longevity. Most floating mats that developed over shallow water have long ago grounded and developed vegetation that would no longer characterize them as classic peatlands, and therefore they have not attracted the attention of peatland investigators.

Prevalence and importance of floating mats: Mat formation, favored by shelter from waves, is considered to be essential to the development of peatlands in Indiana. This is supported by the stratigraphic and macrofossil data presented by Swinehart & Parker (2000). Significant lenses of open water were found buried within the strata of nearly all 12 peatlands cored (Swinehart & Parker 2000). Although most Indiana peatlands have no lakes remaining, the few that actually exhibit open water are surrounded by a floating mat. Additionally, Lindsey (1932), Smith (1937), Moss (1940), Keller (1943), and Wilcox & Simonin (1988), present evidence of lenses of open water in stratigraphic profiles of other Indiana peatlands. With careful analysis of peatlands exhibiting solid profiles, evidence of a distinction between mat-peat and debris-peat (see Kratz & DeWitt 1986) might indicate the previous presence of a floating mat that has been entirely grounded (hence no lens of open water remains). Some peatlands, however, especially those that develop over marl flats, appear to lack evidence of a previous floating mat (Swinehart 1996b).

Because the development of a floating mat seems to be so important to the establishment and persistence of typical peatland plants in the southern Great Lakes region, some comparisons need to be made between the potential physical and hydrological characteristics of the mat versus the typical littoral situation. Kratz & DeWitt (1986) provide a useful model illustrating the factors controlling mat development on small peatlands. At the oldest (shoreward) portions of the bogs that they studied, where the peat was grounded and all compaction had ceased due to peak density, a state of "equilibrium" occurred in which no net accumulations of peat were noted (productivity was equal to decomposition). In the zones of compaction and thickening (closer to the open water), accumulations of peat at the surface pushed the mat further below the surface of the water table. In this case, biomass produced at the surface would be continually submersed into the inundated, oxygen-poor portion of the mat, preventing complete decomposition and thus creating an increasingly nutrient-poor substrate (see Fig. 2).

If the margins of a lake are disturbed to a considerable extent by waves, flocculent organic detritus will be transported to deeper portions of the basin and will never accumulate about the margins (Fig. 3). Only the more solid or dense sedimentary debris would be deposited, leaving no room for compaction. The organic sediments would eventually exceed the limit of the ground water to harbor sufficient oxygen to allow the rate of decom-

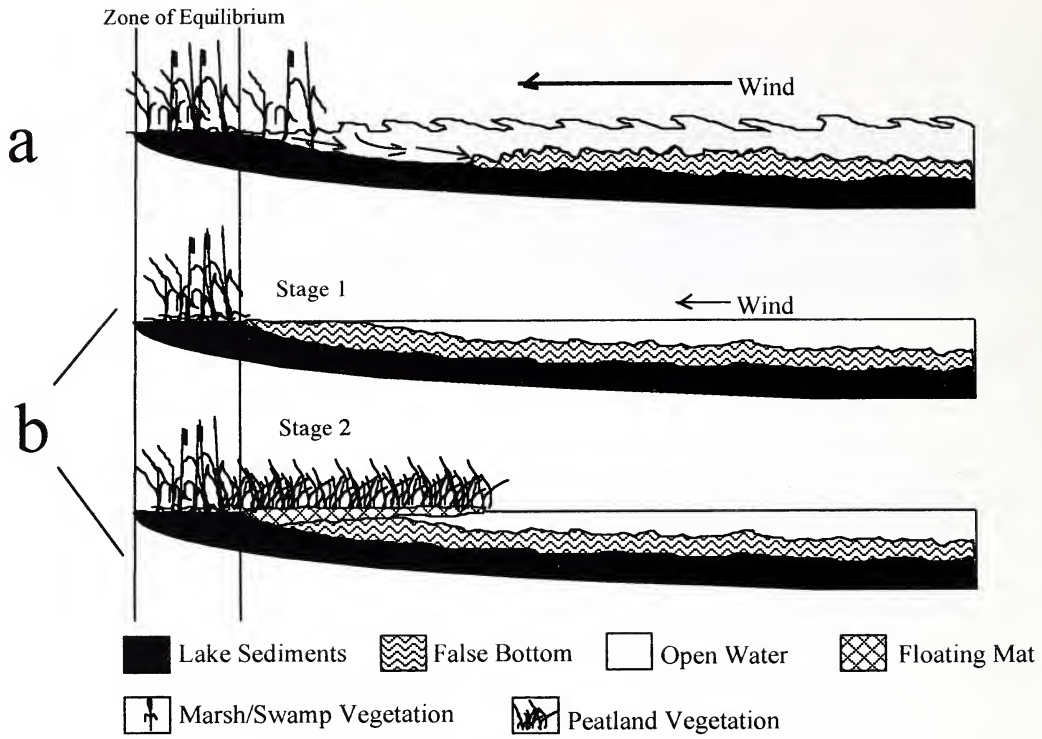

Figure 3.—Conceptual model showing a) wave-battered shore where consolidated lake sediments dominate and flocculent false bottom sediments are transported to deeper water, and b) protected shoreline where flocculent sediments accumulate near shore and provide a treacherous, water-logged substrate where mat-forming plants take hold. The oxygenated "zone of equilibrium" (after Kratz & DeWitt 1986) is where productivity is nearly equal to decomposition; and, consequently, plant available nutrients are more prevalent there.

position to approach the rate of productivity. Since the margins would be fully "grounded," fluctuation of the water table above or below the surface of the sediments would favor oxidation and decomposition. Or, if standing water persisted over the littoral zone, a similar "equilibrium" might occur due to higher oxygen diffusion.

In the case of a protected shore that accumulates appreciable amounts of unconsolidated organic material, enough support is provided for rhizomitous plants to take hold and eventually form a floating matrix or mat (Fig. 3). Once the mat is formed, any seasonal or regional water fluctuations would have little or no effect on the mat. The mat and its associated flora would rise and fall with the water. In this situation, most of the mat is continually inundated, oxygen-poor, and thus exhibits productivity which greatly exceeds decomposition. Only when the mat is grounded to the point where compaction no longer occurs does the productivity at the surface begin to equal decomposition (Kratz & DeWitt 1986).

While the vegetation of a pioneering mat often supports characteristic peatland plants, it may harbor just as many typical marsh species, such as *Thelypterus palustris*, *Typha* spp., *Scirpus validus*, and *S. acutus* (Swinehart & Parker 2001). Only after the chemistry of the substrate has been altered sufficiently via anoxia, cation exchange, and loss of plant-available nutrients does the mat take on a unique or characteristic peatland flora.

Drainage, mineral richness, stratigraphy, and vegetation: Peatlands do not develop at the same rate in all basins that happen to be favorable to peat formation. Lake, fen, and bog sediments occupy varying proportions of the total volume of a given basin. However, based on stratigraphy and radiocarbon dating,

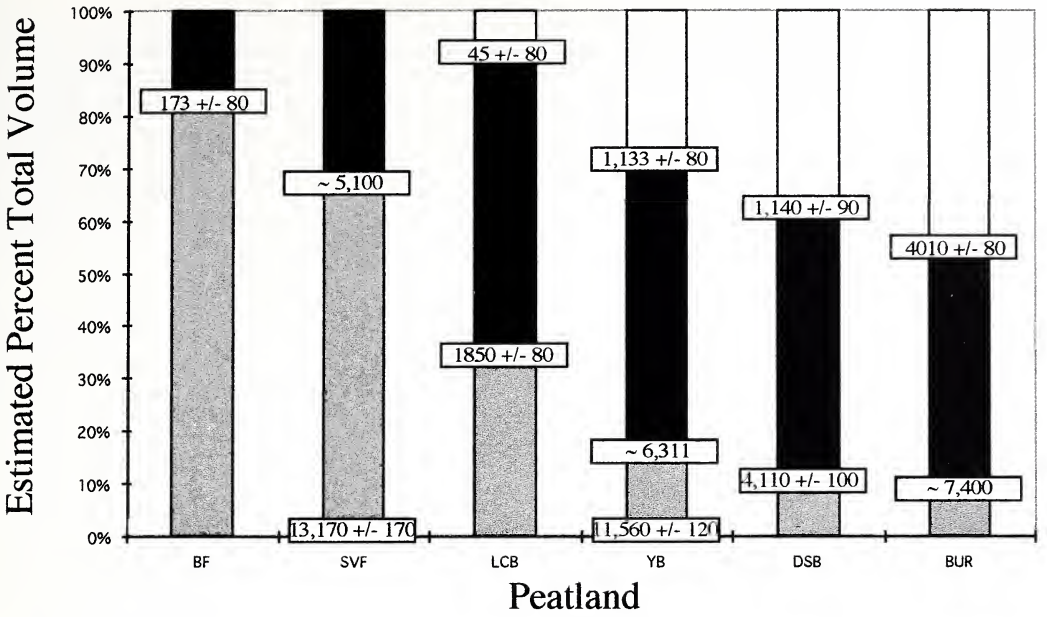

Figure 4.—Stratigraphy and associated radiocarbon (^{14}C) dates of six kettles in relation to percent total volume. BF = Binkley Fen, SVF = Svoboda Fen, LCB = Little Chapman Bog, YB = Yost Bog, DSB = Dutch Street Bog, BUR = Burket Bog. BF and SVF are alkaline fens, LCB is a transitional peatland; and YB, DSB, and BUR are leatherleaf bogs. Radiocarbon dates preceded by "~" are estimated. White bar is sphagnum peat, black bar is fen peat, and gray bar is lake sediment.

leatherleaf (*Chamaedaphne calyculata*) dominated peatlands made the transition from lake to peatland between 2250–5550 ^{14}C ybp earlier than other types of peatlands, both *Sphagnum*-dominated and non-*Sphagnum*-dominated (Fig. 4). Estimated percent total volume of lake sediments in three leatherleaf bogs ranged from 15–17%. Lake sediments were superceded by fen peat, which occupied from 40–55% of the total volume of the basins of leatherleaf bogs. *Sphagnum*-peat in the leatherleaf bogs occupied from 28–45% of the total volume of the basins. The basin occupied by Little Chapman Bog, a transitional peatland (between fen and bog), was composed of 37% lake sediments, 53% fen sediments, and 10% *Sphagnum*-peat. Two fens, Binkley and Svoboda, lacked a layer of *Sphagnum*-peat. The total in their basins (given respectively) included 82% and 66% lake sediments and 18% and 34% fen sediments.

If all of the basins, regardless of size or depth, began with their water-level at the same elevation as it is today, and all of them were proportionally equal in terms of watershed size, productivity, hydrology, and mineral richness, it could be expected that the proportion of the volume where transition from lake to peatland occurred would be equal among the basins. Since this is not the case, several external factors must be examined.

Because peat has its origins at the interface between air and the water surface, it can be deduced that the transition from sediments to peat coincides with the accumulation of lake sediments to the surface of the water, at least around the margins. Although some peat will be transported by currents from the margins to the deeper areas (where coring is conducted), the transition point in the profile is likely to be relatively close to where the water surface was at the time of peat initiation. This may explain why so little volume is occupied by lake sediments in the leatherleaf bogs. At the time of their formation (probably as a result of the nature of the substrate and hydrology), the water level in the basins was much shallower than at present, and the majority of their volume began to fill with lake sediments at an earlier time. As these sediments accumulated, drainage was further impeded (see Crum 1988), and water-levels slowly rose. In-

stead of sprawling over a shallow bench, steep upland slopes of the local watershed confined the growing peatland to a small, deep area.

The fens, on the other hand, appear to have begun with more water occupying their basins. More time was required for the sediments to accumulate to the point where they reached the surface; and hence the point at which peat began to form was delayed, and most of the basin filled with lake sediments. Three qualities distinguished the two basin-type fens from the *Sphagnum*-bogs: 1) fen basins were not lined with continuous, appreciable amounts of clay, 2) the watersheds of fens were hundreds of times greater than the area of the respective wetland, and 3) the fens possessed inlets and/or outlets. In contrast, bogs had significant and nearly continuous deposits of silt and clay (up to 4 m in Dutch Street Bog) lining the basin, their watersheds ranged from only 2–4 times the area of the respective wetland, and none possessed inlets or outlets.

Morphometry of the basin itself seems to have little effect on the vegetation that eventually develops on the peat. While it has been demonstrated that most peatlands in Indiana senesce into red maple-dominated lowland forests (Swinehart & Parker 2000, 2001), the pathway to that end is not the same for all peatlands. Palaeoecological evidence shows that in some extremely mineral-rich fens, the open mat is invaded simultaneously by trees and *Sphagnum* hummocks such that an open *Sphagnum* bog never develops (Swinehart & Parker 2000). This is already apparent at Svoboda Fen. Binkley Fen, although mineral-rich, is developing areas on the open mat that are becoming *Sphagnum*-dominated while there is no immediate evidence or threat of forest encroachment. Little Chapman Bog, which in recent times has developed an open, *Sphagnum*-dominated condition (with no low shrub component), is quickly succumbing to tall shrubs and wetland trees.

At the mineral-poor end of the spectrum are the leatherleaf bogs. None in the present study show any evidence, palaeoecological or otherwise, of having harbored typical bog conifers such as tamarack (Swinehart & Parker 2000). They simply succeed from low shrub bogs to tall shrub bogs (dominated by *Vaccinium corymbosum*) and finally to red maple-dominated forests (Swinehart & Parker 2001). Whether or not alkaliphobic species such as *Sphagnum* ever develop is dependent on the resistance of the ecosystem to the influence of mineral-rich groundwater. While the morphometric qualities that favor the simple genesis of peat seem to be the same for all basins, factors such as hardpan permeability, watershed area, and hydrologic history most likely determine the composition and structure of the successive stands of vegetation.

CONCLUSIONS

The factors affecting the formation and distribution of peatlands in the southern Great Lakes region are clearly hierarchical. At the coarsest level, glacial processes such as the stagnation of entire lobes of ice facilitated the formation of kettles. The local processes that determined the texture and composition of the drift affected drainage. Size, shape, and position of individual ice masses greatly affected the limnology of resulting lakes. And, at the finest level, biological responses to these abiotic factors resulted in variation in the composition, structure, and succession of the vegetation that eventually colonized the glacial lakes.

The only significant feature separating peat-forming kettles from non-peat-forming kettles was surface area. Small basins seemed most likely to become peat-forming due to reduced wind and wave-induced erosion. Protected shores were more likely to develop a floating mat that favored the genesis and build-up of peat. The chemistry and ecology of the successive stands of vegetation that eventually colonized the peat were most affected by watershed area and hardpan permeability (which ultimately determined the degree of minerotrophy).

Experimental research is needed to further investigate the role of waves and basin morphometry on littoral ecology and peatland formation.

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LITERATURE CITED

Andreas, B.K. & G.R. Bryan. 1990. The vegetation of three *Sphagnum*-dominated basin-type bogs in northeastern Ohio. Ohio Journal of Science 90: 54–66.

Andreas, B.K. & J. Knoop. 1992. 100 years of change in Ohio peatlands. Ohio Journal of Science 92:130–138.

Coburn, H., D. Dean & G.M. Grant. 1932. An ecological study of Bryant's Bog, Cheboygan County, Michigan. Papers of the Michigan Academy of Sciences, Arts & Letters 18:57–65.

Cole, G.E. 1983. Textbook of Limnology. 3rd ed. C.V. Mosby Co., St. Louis. 401 pp.

Crum, H.A. 1988. A Focus on Peatlands and Peatmosses. University of Michigan Press, Ann Arbor, 306 pp.

Davis, C.A. 1907. Peat: Essays on Its Origin, Uses, and Distribution in Michigan. Ph.D. Dissertation, University of Michigan, Ann Arbor. 179 pp.

Gates, F.C. 1942. The bogs of northern lower Michigan. Ecological Monographs 12:213–254.

Glime, J.M., R.G. Wetzel & B.J. Kennedy. 1982. The effects of bryophytes on succession from alkaline marsh to *Sphagnum* bog. American Midland Naturalist 108:209–223.

Hamp, F.A. 1940. A fossil pollen study of two northern Indiana bogs. Butler University Botanical Studies 4:217–225.

Howell, J.W. 1938. A fossil pollen study of Kokomo Bog, Howard County, Indiana. Butler University Botanical Studies 4:117–127.

Hutchinson, G.E. 1975. A Treatise on Limnology, Vol. 1, Part 1 - Geography and Physics of Lakes. John Wiley & Sons, New York. 540 pp.

Karlin, E.F. & L.M. Lynn. 1988. Dwarf-shrub bogs of the southern Catskill Mountain region of New York State: Geographic changes in the flora of peatlands in northern New Jersey and southern New York. Bulletin of the Torrey Botanical Club 115:209–217.

Keller, C.O. 1943. A comparative pollen study of three Indiana bogs. Butler University Botanical Studies 6:65–80.

Kratz, T.K. & C.B. DeWitt. 1986. Internal factors controlling peatland-lake ecosystem development. Ecology 67:100–107.

Lerman, A. (ed.). 1978. Lakes—Chemistry, Geology, Physics. Springer-Verlag, New York. 363 pp.

Lindsey, A.J. 1932. The Merrillville white pine (*Pinus strobus*) Bog, Lake County,Indiana. Butler University Botanical Studies 2:179–182.

Miller, N.G. & R.P. Futyma. 1987. Paleohydrological implications of Holocene peatland development in northern Michigan. Quaternary Research 27:297–311.

Moss, B.W. 1940. A comparative pollen study of two bogs within the boundaries of the late-Wisconsin glaciation in Indiana. Butler University Botanical Studies 4:207–216.

Otto, J.H. 1938. Forest succession of the southern limits of early Wisconsin glaciation as indicated by a pollen spectrum from Bacon's Swamp, Marion County, Indiana. Butler University Botanical Studies 4:93–116.

Prettyman, R.L. 1937. Fossil pollen analysis of Fox Prairie Bog, Hamilton County, Indiana. Butler University Botanical Studies 4:33–42.

Richards, R.R. 1938. A pollen profile of Otterbein Bog, Warren County, Indiana. Butler University Botanical Studies 4:128–140.

Rigg, G.B. & C.T. Richardson. 1934. The development of *Sphagnum* bogs in the San Juan Islands. American Journal of Botany 21:610–622.

Rigg, G.B. & C.T. Richardson. 1938. Profiles of some *Sphagnum*-bogs of the Pacific Coast of North America. Ecology 19:408–434.

Ruttner, F. 1953. Fundamentals of Limnology. 3rd ed. University of Toronto Press, Toronto.

Sanderlin, L.W. 1984. Uncle Larry's Lake Maps [USGS lake-contour maps]. Larry W. Sanderlin. 323 pp.

Scott, W. 1916. Report on the lakes of the Tippecanoe Basin (Indiana). Indiana University Studies 3(31):39 pp., 13 maps.

Scott, W. & D.H. Miner. 1936. Sedimentation in Winona Lake and Tippecanoe Lake, Kosciusko County, Indiana, July 31, 1930, to July 30,1935. Proceedings of the Indiana Academy of Science 45:275–286.

Smith, W.M. 1937. Pollen spectrum of Lake Ciscott Bog, Cass County, Indiana. Butler University Botanical Studies 4:43–54.

Swan, J.M.A. & A.M. Gill. 1970. The origins, spread, and consolidation of a floating bog in Harvard Pond, Petersham, Massachusetts. Ecology 51:829–840.

Swickard, D.A. 1941. Comparison of pollen spectra from bogs of early and late Wisconsin glaciation in Indiana. Butler University Botanical Studies 5:67–84.

Swinehart, A.L. 1996a. Fishes of the inland waters of Beaver Island, Charlevoix County, Michigan. Proceedings of the Indiana Academy of Science 105:207–216.

Swinehart, A.L. 1996b. Palaeoecology of the Wilkinson Giant Beaver Locality, Whitley County, Indiana. Report to the Indiana Dept. of Natural Resources, Indiana State Museum. 19 pp.

Swinehart, A.L. 1997. The Development and Ecology of Peatlands in Indiana. Ph.D. Dissertation, Purdue University, Dept. of Forestry & Natural Resources, West Lafayette, Indiana. 303 pp.

Swinehart, A.L. & G.R. Parker. 2000. Palaeoecology and development of peatlands in Indiana. American Midland Naturalist 143:267–297.

Swinehart, A.L. & G.R. Parker. 2001. The struc-

ture and composition of the vegetation in the lake-fill peatlands of Indiana. Proceedings of the Indiana Academy of Science 110:51–78.

Taylor, A.E. 1907. The peat deposits of northern Indiana. Annual Report of the Indiana Department of Geology and Natural Resources 31:73–298.

Transeau, E.N. 1905. The bogs and bog flora of the Huron River Valley. Botanical Gazette 11: 351–448.

Wayne, W.J. 1966. Ice and land: A review of the Tertiary and Pleistocene history of Indiana. *In* Natural Features of Indiana. (A.A. Lindsey, ed.). Indiana Academy of Science, Indianapolis. 600 pp.

Welch, P.S. 1952. Limnology. 2nd ed. McGraw-Hill Book Co. New York. 538 pp.

Welch, P.S. 1936. Limnological investigation of a strongly basic bog lake surrounded by an extensive acid-forming bog mat. Papers of the Michigan Academy of Sciences, Arts & Letters 21: 727–751.

Welch, P.S. 1938a. A limnological study of a retrograding bog lake. Ecology 19:435–453.

Welch, P.S. 1938b. A limnological study of a bog lake which has never developed a marginal mat. Transactions of the American Microscopical Society 57:344–357.

Welch, P.S. 1939. Vertical distribution of summer temperature in the false bottoms of certain Michigan bog lakes. Ecology 20:38–46.

Wetzel. R.G. 1983. Limnology. 2nd ed. Saunders College Publishing, Fort Worth. 767 pp.

Wilcox, D.A. & H. Simonin. 1988. The stratigraphy and development of a floating peatland, Pinhook Bog, Indiana. Wetlands 8:75–91.

Wilson, I.T. 1938. The accumulated sediment in Tippecanoe Lake and a comparison with Winona Lake. Proceedings of the Indiana Academy of Science 47:234–253.

Manuscript received 21 March 2001, revised 24 March 2002.

2002. Proceedings of the Indiana Academy of Science 1:45–55

THE IMMUNOSUPPRESSIVE EFFECT OF SIDESTREAM SMOKE ON THE CONTACT HYPERSENSITIVITY RESPONSE TO THE HAPTEN DINITROFLUORBENZENE IN BALB/c MICE

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ABSTRACT. In recent years, there have been increasing reports regarding the impact of various stressors on the immune system. It is well established that epicutaneous application of haptens can induce contact hypersensitivity (CHS), a delayed-type immune response. Certain irritants such as ultraviolet B have been shown to induce CHS tolerance. In this study, using the ear swelling assay and the hapten dinitrofluorbenzene (DNFB), we produce evidence suggesting that sidestream cigarette smoke may alter the immune system of the skin of BALB/c mice in a way that results in CHS suppression. Mice were divided into three control and three dosage groups consisting of daily exposure to sidestream smoke from one filter-tip cigarette. Ear swelling of positive controls was significantly greater ($P<0.05$) than for all other groups except the pre-challenged experimental mice ($P<0.20$). Significant CHS suppression occurred in both the three-week experimental mice (80.4%; $P<0.001$), and pre-sensitized mice (18.1%; $P<0.01$).

Keywords: Immunosuppression, sidestream smoke, contact hypersensitivity, dinitrofluorbenzene (DNFB)

Immunotoxicity, which examines how various substances undermine the immune system, is a recent and burgeoning field (Bower 1999). One form of immunity that has been well established since the studies of Landsteiner & Jacob (1935) is contact hypersensitivity (CHS). CHS is a T cell-mediated immune response in the epidermis to a reactive hapten covalently coupled to cell surface proteins (Rowden et al. 1977; DiIulio et al. 1996). Hapten-specific T cells are primed by Langerhans cells (LC) which migrate from the sensitized epidermis to the skin-draining lymph nodes (Kripke et al. 1990; Wang et al. 1997). Subsequent challenges with the hapten results in cutaneous infiltration of the primed T cells and their activation to produce various cytokine mediators of CHS such as tumor necrosis factor-α (TNF-α) (Enk & Katz 1991).

During antigen priming, CD^+ T cells develop from Th0 precursor cells into either CD8 super (+) T (Th1) cells which produce inflammatory cytokines such as interleukin-2 (IL-2) and interferon-gamma (IFN-γ) or CD4 super (+) T (Th2) cells which produce anti-inflammatory cytokines such as interleukin-4 (IL-4) and interleukin-10 (IL-10) (DiIulio et al. 1996; Niizeki & Streilein 1997; Nagai et al. 2000; Simkin et al. 2000). Th1 cells are the effector cells of cell-mediated immunity such as delayed-type hypersensitivity (DTH) and CHS, whereas Th2 cells provide signals enhancing antibody production (Cher & Mosmann 1987). Differentiation of Th0 cells to the Th1 or Th2 phenotype is regulated by the cytokine environment during antigen priming. Th2 cell development requires IL-4 and Th1 cell development is promoted by interleukin-12 (IL-12) (Aragane et al. 1994; Schmitt et al. 1995).

The skin serves as a complex barrier separating the internal compartments from the external environment, including bacteria, viruses, fungi and environmental toxins (Rheins et al. 1993). The effect of skin exposure to ultraviolet light has been examined extensively. Numerous studies have focused on the effects of ultraviolet B (UVB) radiation on CHS. The induction of tolerance to CHS is a common finding (Kurimoto et al. 1994; Smith et al. 1997). Other environmental agents have also been shown to suppress CHS (Blaylock et al. 1993; Ullrich 1994; Schmitt et al. 1995; Tam et al. 1997).

One environmental irritant that the skin could encounter is sidestream smoke. Environmental tobacco smoke (ETS), in an average room of active smokers, is composed of

approximately 85% sidestream smoke (Fielding & Phenow 1988). Mainstream and sidestream smoke both contain a large number of chemical carcinogens and other toxic substances; but undiluted sidestream smoke carries many compounds, such as ammonia, benzene, carbon monoxide, and nicotine, in far greater concentrations (USDHHS 1986). In order to address the potential of this agent as a modulator of the immune system, we investigated the effect of sidestream smoke on the induction (sensitization) and elicitation (challenge) phases of CHS using the mouse ear swelling assay. Our results suggest that ear swelling is significantly suppressed by sidestream smoke in BALB/c mice, and appears to be related to the number of days of exposure prior to sensitization.

METHODS

Mice.—Female BALB/c mice were purchased from Harlan Sprague Dawley (Indianapolis, Indiana) at six weeks of age and used at 8–12 weeks of age. They were maintained in an environment controlled for temperature and light and allowed free access to food and water.

Ear swelling protocol.—The method of Phanuphak et al. (1974) as modified by Tamak et al. (1981) was used to quantify the ear swelling response to contact allergen (Table 1). Mice were randomized into 6 groups (3 control and 3 experimental) ranging in sample size from 18–30. Five of the six groups, including nonsmoke-exposed positive control mice (PC), were sensitized by topical application of 20 μl of 0.5% of the hapten dinitrofluorobenzene (DNFB) (Sigma, St. Louis, Missouri) in a 4:1 acetone/olive oil mixture onto their shaved abdominal surface on day 0 and day 1. Negative control (NC) mice were mock-sensitized with DNFB solvent. On day 5, five of the six groups were challenged with 20 μl of 0.2% DNFB, distributed equally, on both sides of the right ear. Background control (BC) mice were mock-challenged with DNFB solvent. After 24, 48, and 72 h, ear thickness measurements of all mice were made with an engineer's micrometer (Fisher Scientific, Burr Ridge, Illinois); and the CHS response to DNFB was assessed by subtracting post-challenge from pre-sensitized values.

Smoking procedure.—One of the three experimental groups was exposed to sidestream smoke for three weeks prior to sensitization through 72 h post-challenge. This group was designated as 3-week experimentals (3WE). A second group was exposed to sidestream smoke from day 0 (prior to sensitization) through 72 h post-challenge, and was designated as pre-sensitized experimentals (PSE). A third group was exposed to sidestream smoke from day 5 (prior to challenge) through 72 h post-challenge, and was designated as pre-challenged experimentals (PCE). Smoke exposure occurred in acrylic plastic (Plexiglas™) chambers (25.5 × 30.5 × 21.0 cm) containing six airholes 6.5 mm in diameter on two opposite sides. Mice received a 40 min exposure to sidestream smoke from one commercial brand filter-tip cigarette each day of their respective smoking regimen. The cigarettes employed contained tar and nicotine contents of 15.1 mg and 0.13 mg, respectively (Federal Trade Commission 1997).

Assessment of hyporesponsiveness.—The degree of hyporesponsiveness was assessed by calculating the percent suppression of CHS according to the formula below reported by Sauder et al. 1981.

$$\% \text{ Suppression} = \{1 - [(\text{Experimentals} - \text{Negative controls}) \div (\text{Positive controls} - \text{Negative controls})]\} \times 100$$

Values for experimentals, positive controls, and negative controls represent differences in ear swelling (mm × 10^{-2}) produced by the above ear swelling protocol.

Statistical analysis.—Mean differences in ear swelling were analyzed using ANOVA and Tukey Multiple Comparison tests (Zar 1999). The Student *t* test was used to assess the degree of reactivity. A *P* value of less than 0.05 was considered significant.

RESULTS

Six groups of BALB/c mice were compared to determine the effect of sidestream smoke on CHS (Table 1). All groups, except negative control mice, were sensitized with 20 μl of 0.5% DNFB on shaved abdomens on days 0 and 1. All groups, except background control mice, were challenged on the right ear with 20 μl of 0.2% DNFB on day 5. Ear pinna

Table 1.—Protocol used to determine the effects of sidestream smoke on DNFB hapten-induced contact hypersensitivity of BALB/c mice. [1]3-week experimental (3WE) mice were exposed to sidestream smoke from 3 weeks prior to sensitization (Day 0) to 72 h post-challenge (Day 8). [2]Pre-sensitized experimental (PSE) mice were exposed to sidestream smoke from day of sensitization (Day 0) to 72 h post-challenge (Day 8). [3]Pre-challenged experimental (PCE) mice were exposessd to sidestream smoke from day of right ear challenge (Day 5) to 72 h post-challenge (Day 8). [4]Negative control (NC) mice were mock sensitized with DNFB solvent of 4 parts acetone:1 part olive oil. [5]Background control (BC) mice were mock challenged with DNFB solvent of 4 parts acetone:1 part olive oil.

	Treatment					
Test group	Day 0	Day 1	Day 5	Day 6	Day 7	Day 8
Positive Control (PC)	Sens 1 (0.5% DNFB)	Sens 2 (0.5% DNFB)	Challenge (0.2% DNFB)	24 h EAr Measurement	48 h Ear Measurement	72 h Ear Measurement
3-week Experimental[1] (3WE)	Sens 1 (0.5% DNFB)	Sens 2 (0.5% DNFB)	Challenge (0.2% DNFB)	24 h Ear Measurement	48 h Ear Measurement	72 h Ear Measurement
PS Experimental[2] (PSE)	Sens 1 (0.5% DNFB)	Sens 2 (0.5% DNFB)	Challenge (0.2% DNFB)	24 h Ear Measurement	48 h Ear Measurement	72 h Ear Measurement
PC Experimental[3] (PCE)	Sens 1 (0.5% DNFB)	Sens 2 (0.5% DNFB)	Challenge (0.2% DNFB)	24 h Ear Measurement	48 h Ear Mesurement	72 h Ear Measurement
Negative Control[4] (NC)	Mock Sens 1 (DNFB solvent)	Mock Sens 2 (DNFB solvent)	Challenge (0.2% DNFB)	24 h Ear Measurement	48 h Ear Measurement	72 h Ear Measurement
Background Control[5] (BC)	Sens 1 (0.5% DNFB)	Sens 2 (0.5% DNFB)	Mock Challenge (DNFB solvent)	24 h Ear Measurement	48 h Ear Measurement	72 h Ear Measurement

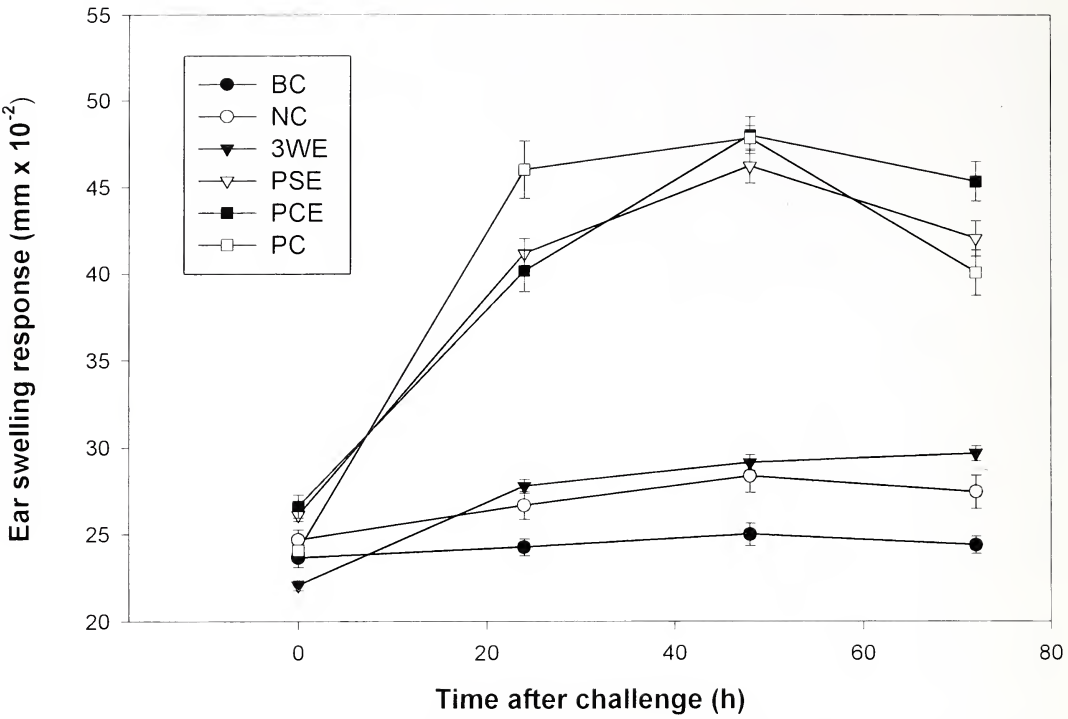

Figure 1.—Effect of sidestream smoke on contact hypersensitivity response of BALB/c mice to DNFB. Values are means ± SEM. Maximum swelling for all test groups was 48 h post-challenge. BC = background controls (n = 20), NC = negative controls (n = 21), 3WE = smoke-exposed mice from three weeks presensitization to 48 h postchallenge (n = 18), PSE = smoke-exposed mice from day of sensitization to 48 h postchallenge (n = 28), PCE = smoke-exposed mice from day of challenge to 48 h postchallenge (n = 21), PC = positive controls (n = 18).

thickness measurements for each group were recorded on day 6 (24 h post-challenge), day 7 (48 h post-challenge), and day 8 (72 h post-challenge).

A dose response curve showed that maximum ear swelling occurred at 48 h post-challenge for all six groups (Fig. 1). Ear measurements were recorded from day 0 (pre-sensitization) through day 8 (72 h post-challenge). No significant difference in ear swelling was noted from day 0 to day 5 (pre-challenge) (Table 2). Mean ear swelling for the three control groups at 48 h was 23.77 mm $\times 10^{-2}$ (98.7%) for PC mice, 3.67 mm $\times 10^{-2}$ (14.9%) for NC mice, and 1.35 mm $\times 10^{-2}$ (5.7%) for BC mice. The three experimental groups produced a mean ear swelling of 21.38 mm $\times 10^{-2}$ (80.3%) for PCE mice, 20.11 mm $\times 10^{-2}$ (77.0%) for PSE mice, and 7.07 mm $\times 10^{-2}$ (32.0%) for 3WE mice. The increase in ear thickness of PC mice was significantly greater than that of all other groups ($P<0.01$), except for the PCE mice ($P<0.20$). Significant CHS suppression occurred in both 3WE (80.4%; $P<0.001$) and PSE mice (18.1%; $P<0.01$) (Fig. 2).

DISCUSSION

The skin has become a convenient site to study the complexities of the immune response. Because the skin is the largest and most exposed organ of the body, it comes in contact with an extensive array of environmental insults such as toxins, allergens and irritants (Rheins et al. 1993). One potential environmental irritant that the skin might encounter is that of sidestream tobacco smoke. CHS is a delayed-type immune response (Asherson & Ptak 1968) and has served as a useful model for investigating the allergen-specific immune responses of T cells and skin-associated antigen-presenting cells (APC) (Nuriya et al. 1996). In order to address whether it is possible for sidestream smoke to

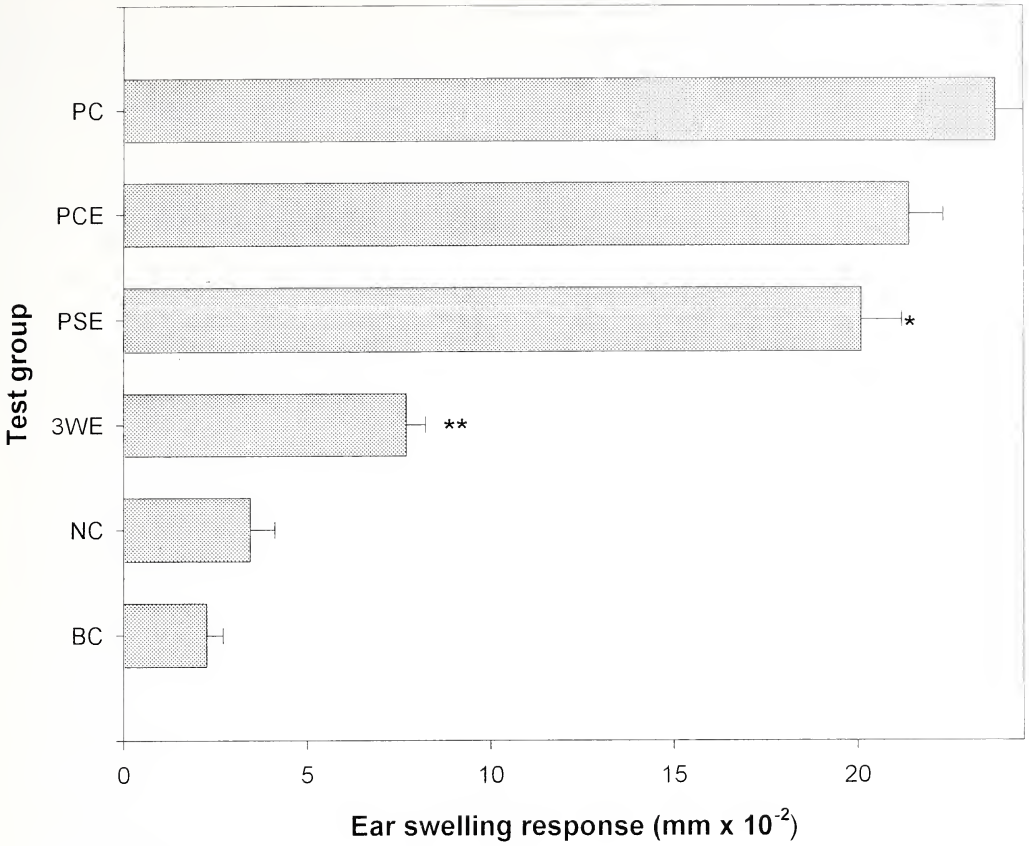

Figure 2.—Maximum ear swelling of BALB/c mice. Test groups are background controls (BC), negative controls (NC), three-week experimentals (3WE), pre-sensitized experimentals (PSE), pre-challenged experimentals (PCE), and positive controls (PC). Values are means ± SEM; n = 18–30/test group (see Table 2). Ear swelling of positive controls was significantly greater ($P<0.05$) than for all other groups, except the pre-challenged experimentals. Asterisks indicate significance of percent suppression of contact hypersensitivity (*$P<0.01$, **$P<0.001$).

impact the immune system, we examined the effect of this agent on the induction and elicitation of CHS using the mouse ear swelling assay.

There are numerous studies that have illustrated a variety of deleterious effects produced by sidestream smoke exposure on mammalian systems. In humans, these include low birth weight of offspring born to mothers exposed to sidestream smoke during pregnancy (Martin & Bracken 1986), respiratory dysfunction (White & Froeb 1980), cardiovascular ailments (Aronow 1978; Garland et al. 1985) and increased incidence of cancer (Correa et al. 1983; Wigle et al. 1987). Nonhuman animal studies have also demonstrated many negative effects of sidestream smoke exposure (Mays et al. 1997; Resnik & Marquard 1980). In this investigation, we produce evidence that sidestream cigarette smoke may alter the immune system of the skin in a way which results in an increased unresponsiveness or tolerance to CHS. Experimental BALB/c mice were exposed to sidestream smoke for varying periods of time. One group (3WE) was exposed to sidestream smoke daily for three weeks prior to sensitization with the hapten DNFB. A second group (PSE) was exposed to sidestream smoke for the first time on the day they were sensitized (D0), whereas a third group (PCE) wasn't exposed to sidestream smoke until the day they were challenged with

Table 2.—Ear swelling response. The effects of sidestream smoke on DNFB hapten-induced contact hypersensitivity of BALB/c mice. [1]The increase in ear thickness was measured from day of sensitization (Day 0) to 72 h post-challenge (Day 8). [2]Intergroup ear measurements showed no significant differences between Day 0 (pre-sensitized) and Day 5 (pre-challenged) mice. [3]Maximum ear swelling for all groups occurred at 48 h post-challenge. The increase in ear thickness of positive control mice is significantly greater ($p<0.01$) than that of all other groups at 48 h post-challenge, except for the PC Experimental mice ($p<0.055$). [4]No significant difference from 48 h post-challenge measurement. [5]Mice exposed to sidestream smoke from day of sensitization (Day 0) to 72 h post-challenge (Day 8). [6]Mice exposed to sidestream smoke from day of challenge (Day 5) to 72 h post-challenge (Day 8).

		Increased ear thickness (mm × 10^{-2})[1]						
Test group	*n*	24 h Post-Challenge[2] (+ SEM)	Change (%)	48 h Post-challenge (+ SEM)	Change (%)	72 h Post-challenge (+ SEM)	Change (%)	% Change from 48 h
Positive Control (PC)	18	21.933 (1.34)	+ 91.1	23.766 (0.77)	+ 98.7[3]	15.993 (1.27)	+ 66.5	− 32.2
3-week Experimental (3WE)	30	5.700 (0.45)	+ 25.8	7.066 (0.45)	+ 32.0	7.600 (0.53)	+ 34.4	+ 2.4[4]
PS Experimental[5] (PSE)	28	15.036 (1.01)	+ 57.6	20.107 (1.10)	+ 77.0	15.933 (1.21)	+ 61.0	− 16.0
PC Experimental[6] (PCE)	21	13.521 (1.12)	+ 50.8	21.381 (0.94)	+ 80.3	18.721 (1.06)	+ 70.3	− 10.0
Negative Control (NC)	21	1.976 (0.57)	+ 8.0	3.665 (0.67)	+ 14.9	2.764 (0.78)	+ 11.2	− 11.2
Background Control (BC)	20	0.600 (0.44)	+ 2.5	1.350 (0.44)	+ 5.7	1.036 (0.52)	+ 3.1	− 2.6

DNFB (D5). The 3WE mice were the least responsive to CHS with only a 32% increase in ear swelling. The PSE mice showed a 77% increase in ear swelling, and the PCE mice had an increase in ear swelling of 80.3%. The degree of ear swelling of both the 3WE and PSE mice was significantly less than that of naive (PC) mice ($P<0.01$), which had an ear swelling increase of 98.7%. The ear swelling response of PCE mice was not significantly less than the PC mice ($P<0.20$). The degree of immunosuppression showed a similar pattern. The CHS response was suppressed by 80.4% in the 3WE mice ($P<0.001$) and 18.1% in the PSE mice ($P<0.01$), indicating that sidestream smoke exposure can induce immunotolerance in BALB/c mice. These results are similar to those observed for ICR mice, in which CHS of 3WE mice was suppressed by 80.8%. However, neither the PSE nor PCE mice showed significant CHS suppression (Mays & Mays 1999).

It was not the purpose of this study to determine the cause of the observed immunosuppression. However, other studies regarding CHS offer some possible explanations. For the epidermis to produce the optimal toxicologic, immunologic and biochemical barrier, each of the major cell types of this tissue, including keratinocytes (KC) and Langerhans cells (LC) must function together in a dynamic and integrated fashion (Rheins et al. 1993). Epidermal/dermal intercellular biochemical signals (e.g., interleukins, intercellular adhesion molecules, growth factors, etc.) produced by these cells provide skin with local homeostatic signals to ensure it's integrity when exposed to a variety of insults, including those leading to common inflammatory dermatoses, such as irritant CHS (Baadsgaard & Wang 1991; Murayama et al. 1997). Induction of CHS is a multistep process that begins when a highly reactive hapten (e.g., DNFB) is applied to the cutaneous surface (Kurimoto et al. 1994). The initiation of the immune response requires presentation of antigen in the context of MHC class II molecules to the appropriate T cell clones (Unanue 1984). It is possible that sidestream smoke interferes with this initial antigen-presenting process.

Another potential factor affecting immunosuppression is the role of epidermal Langerhans cells (LC). Interest in cutaneous immune reactions was stimulated in 1977 by the discovery that LC express surface markers characteristic of cells of the macrophage-monocyte lineage (Klareskog et al. 1977). LC possess Ia^+ antigens, and are generally thought to be APC of the skin (Rowden et al. 1977). It is now known that epidermal LC are critical for the induction of CHS to simple chemicals and for the induction of allogenic T cell responses (Toews et al. 1980; Shimada et al. 1987; Manome et al. 1999). Blaylock et al. (1993) showed that a 30 ng application of T-2 mycotoxin produced a 44% suppression of ear swelling in BALB/c mice. Their findings further suggested that the T-2 toxin significantly decreased both MHC class II (Ia) antigen expression on LC, and antigen presentation to T cells. Perhaps sidestream smoke also has a suppressive effect on Ia^+ expression and hapten presentation to T cells.

Sidestream smoke might also produce immunosuppression at some later stage in the immune response process. Skin LC are immature dendritic cells (DC) that form an extensive network in the epidermis, and upon exposure to noxious stimuli such as contact sensitizers (e.g., DNFB), they enter the lymphatics and migrate into T cell zones of lymph nodes to become interdigitating DC (Tang & Cyster 1999). For mature DC to function in an immunogenic manner, it is important that they rapidly interact with antigen-specific T cells in the paracortical area (Bigby et al. 1989; Bottomly 1999). One mechanism that appears to enhance encounters between DC and T cells is for DC to produce T cell attracting chemokines. DC up-regulation of macrophage-derived chemokine (MDC) has been shown to preferentially attract antigen-specific T cells, but not naive T cells (Tang & Cyster 1999). Recently, it was reported that DC exist in at least two forms. Myeloid-like cells (DC1) produce abundant IL-12 and induce a Th1 response, and lymphoid-like cells (DC2) induce a Th2 response. In addition, T helper cells may themselves regulate Th1 and Th2 responses by determining the survival of the appropriate DC subset (Rissoan et al. 1999). Th1 and Th2 responses are produced by the two subsets of T helper cells. Th1 and Th2 cells are determined by the type of cytokine/growth factor secretions in response to antigens (Simon et al. 1991; Xu et al. 1997a; Krasteva et al. 1998). Th1 cells secrete IL-2, IFN-γ, and lymphotoxin, and are primarily as-

sociated with macrophage activation and delayed-type hypersensitivity. Among the interleukins secreted by Th2 cells are IL-4, IL-5, IL-6, and IL-10. These T helper cells are normally B cell activators. Both types of T cells secrete IL-3, granulocye-macrophage colony stimulating factor (GM-CSF), TNF-α, and several other induction-specific proteins (Mosmann et al. 1986; DiIulio et al. 1996). It has been shown that the Th1 product IFN-γ inhibits proliferation of Th2 clones in vitro (Gajewski & Fitch 1988), and Th2 clones produce a protein called cytokine synthesis inhibitory factor (CSIF) that inhibits the synthesis of several cytokines by Th1 clones (Fiorentino et al. 1989). Thus, sidestream smoke could have a dual immunosuppressive influence by inhibiting Th1 cytokine production (Th1 response) and stimulating the production of the Th2 cytokine CSIF.

In addition to LC-T cell interaction, keratinocytes (KC), which are the major constituents of the epidermis, are well known for their capacity to secrete a variety of cytokines and growth factors. One KC-produced cytokine is IL-12 which, until recently, was believed to be produced exclusively by macrophages and B cells (Schwarz 1995). IL-12 is known to shift T helper cell response to a Th1 cytokine profile (Xu et al. 1998) and stimulate the production of IFN-γ (Trinchieri 1994; Maguire 1995). IL-12 is required in both the sensitization and challenge phases to produce maximum CHS, and neutralization of IL-12 during sensitization induces hapten-specific tolerance (Riemann et al. 1996; Schwarz et al. 1996). Another cytokine that has received attention is IL-10. Although it was previously considered to be produced primarily by Th2 cells, evidence now indicates that KC also produce IL-10, and that KC-derived IL-10 has an important immunoregulatory function (Enk & Katz 1992). IL-10 converts LC from being potent inducers of primary immune reactions such as CHS to becoming tolerogenic APC (Enk & Katz 1995). Hapten-sensitized LC express high levels of B7-2 and lower levels of B7-1 costimulators on their surface (Xu et al. 1997b). It has been suggested that IL-10 induces tolerance by downregulating the B7 costimulators on APC (Enk et al. 1993). UV radiation is thought to produce immunosuppression by inducing KC to release IL-10, which inhibits the CHS-stimulatory cytokine IL-12 (Schmitt et al. 1995). The lack of B7 costimulators may interfere with LC-T cell interaction and thereby modulate skin cytokine profiles that leads to CHS suppression (Kondo et al. 1996). Suppressor T cell activation has also been associated with UV light-induced immunosuppression (Baadsgaard et al. 1988; Karpus & Swanborg 1989). Perhaps sidestream smoke produces immunosuppression of CHS in a manner similar to that of UV radiation.

The role of Th2 cells in CHS is not clear, but it appears that Th2-derived IL-4 intensifies CHS suppression 48 h post-challenge (Wiegmann et al. 1997). This may partially explain why our maximum percent suppression occurred at 48 h post-challenge. Mast cells are known to contribute to the induction of CHS by DNFB. This is primarily by the mediation of T lymphocyte recruitment in draining lymph nodes by the production of macrophage inflammation protein (MIP)-1 beta (Wang et al. 1998). Perhaps sidestream smoke inhibits this process by decreasing the number of mast cells or blocks their function. Nitric oxide (NO) is another factor implicated in the development of CHS. Elicitation of CHS response to DNFB is known to stimulate the enzyme nitric oxide synthase (NOS) in both KC and LC. NOS converts the amino acid arginine to NO, which contributes to the ear swelling reaction. Certain agents such as N-methyl-L-arginine (L-NMA), which is an NOS inhibitor, significantly reduced CHS induced by treatment of BALB/c mice with DNFB (Ross et al. 1998). It may be that sidestream smoke somehow interferes with NOS activity leading to immunosuppression.

The process of CHS illicitation is complex, and there are many variables that could be involved in the sidestream smoke-induced immunotolerance observed in our laboratory. Although we are aware of at least one study dealing with the effect of cigarette smoking on the immune system (Jung & Irwin 1999), to our knowledge, the work in our lab, including a preliminary investigation on ICR mice (Mays & Mays 1999) and this study on BALB/c mice, are the first investigations of the effect of sidestream smoke on immunity.

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LITERATURE CITED

Aragane, Y., H. Riemann, R.S. Bhardwaj, A. Schwarz, Y. Sawada, H. Yamada, T.A. Luger, M. Kubin, G. Trinchieri & T. Schwarz. 1994. IL-12 is expressed and released by human keratinocytes and eipdermoid carcinoma cell lines. Journal of Immunology 153:5366–5372.

Aronow, W. 1978. Effect of passive smoking on angina pectoris. New England Journal of Medicine 299:21–24.

Asherson, G. & W. Ptak. 1968. Contact delayed hypersensitivity in the mouse. I. Active sensitization and passive transfer. Immunology 15:405–416.

Baadsgaard, O., D. Fox & K. Cooper. 1988. Human epidermal cells from ultraviolet light-exposed skin preferentially activate autoreactive $CD4^+2H4^+$ suppressor-inducer lymphocytes and $CD8^+$ suppressor/cytotoxic lymphocytes. Journal of Immunology 143:3492–3497.

Baadsgaard, O. & T. Wang. 1991. Immune regulation in allergic and irritant skin reactions. Journal of Dermatology 30:61–72.

Bigby, M., R. Vargas & M. Sy. 1989. Production of hapten-specific T cell hybridomas and their use to study the effect of ultraviolet B irradiation on the development of contact hypersensitivity. Journal of Immunology 143:3867–3872.

Blaylock, B.L., Y. Kouchi, E.E. Comment, P.L. Pollack & M.I. Luster. 1993. Topical application of T-2 toxin inhibits the contact hypersensitivity response in BALB/c mice. Journal of Immunology 150:5135–5143.

Bower, J. 1999. Depressed smokers ride immune downer. Science News 155:358.

Bottomly, K. 1999. T cells and dendritic cells get intimate. Science 283:1124–1125.

Cher, D.J. & T.R. Mosmann. 1987. Two types of murine helper T cell clone. II. Delayed-type hypersensitivity is mediated by Th1 clones. Journal of Immunology 138:3688–3694.

Correa, P., L. Pickle, E. Fontham, Y. Lin & W. Haenzel. 1983. Passive smoking and lung cancer. Lancet 2:595–597.

DiIulio, N.A., H. Xu & R.L. Fairchild. 1996. Diversion CD^+ T cell development from regulatory T helper to effector T helper cells alters the contact hypersensitivity response. European Journal of Immunology 26:2606–2612.

Enk, A. & S. Katz. 1991. Early molecular events in the induction phase of contact hypersensitivity. Proceedings of the National Academy of Sciences 89:1398–1402.

Enk, A. & S. Katz. 1992. Identification and induction of keratinocyte-derived IL-10. Journal of Immunology 149:92–95.

Enk, A., V. Angeloni, M. Udey & S. Katz. 1993. Inhibition of Langerhan's cell antigen presentation function by IL-10. A role for IL-10 in tolerance induction. Journal of Immunology 151: 2390.

Enk, A. & S. Katz. 1995. Contact hypersensitivity as a model for T-cell activation in the skin. Journal of Investigative Dermatology 105:805–835.

Federal Trade Commission. 1997. Report of the tar, nicotine and carbon monoxide yield of 1206 varieties of domestic cigarettes for the year 1994 (July) 62:38536.

Fielding, J.E. & K.J. Phenow. 1988. Health effects of involuntary smoking. New England Journal of Medicine 319:1452–1460.

Fiorentino, D., M. Bond & T. Mosmann. 1989. Two types of mouse T helper cells. IV. Th2 clones secrete a factor that inhibits cytokine production by Th1 clones. Journal of Experimental Medicine 170:2081–2095.

Gajewski, T. & F. Fitch. 1988. Anti-proliferative effect of IFN-gamma in immune regulation. I. IFN-gamma inhibits the proliferation of Th2 but not Th1 murine helper T lymphocyte clones. Journal of Immunology 140:4245–4252.

Garland, C., E. Barrett-Conner, L. Suarez, M. Criqui & D. Wingard. 1985. Effects of passive smoking on ischemic heart disease mortality in nonsmokers: A prospective study. American Journal of Epidemiology 121:645–649.

Jung, W. & M. Irwin. 1999. Reduction of natural killer cytotoxic activity in major depression: Interaction between depression and cigarette smoking. Psychosomatic Medicine 61:263–270.

Karpus, W. & R. Swanborg. 1989. $CD4^+$ suppressor cells differentially affect the production of IFN-γ by effector cells of experimental autoimmune encephalomyelitis. Journal of Immunology 143:3492–3497.

Klareskog, L., U. Tjernlung, U. Forsum & P. Peterson. 1977. Epidermal Langerhans cells express Ia antigens. Nature 268:248–250.

Kondo, S., F. Koosheh, B. Wang, H. Fujisawa & D. Sauder. 1996. Contribution of the CD28 molecule to allergic and irritant-induced skin-reactions in CD28 −/− mice. Journal of Immunology 157:4822–4829.

Krasteva, M., J. Kehren, F. Horand, G. Akiba, G. Choquet, M. Ducluzeau, R. Tedone, J. Garrigue, D. Kaiserlian & J. Nicolas. 1998. Dual role of

dendritic cells in the induction and down-regulation of antigen-specific cutaneous inflammation. Journal of Immunology 160:1181–1190.

Kripke, M.L., C.G. Munn, A. Jeevan, J.M. Tang & C. Bucana. 1990. Evidence that cutaneous antigen-presenting cells migrate to regional lymph nodes during contact hypersensitization. Journal of Immunology 145:2833–2838.

Kurimoto, I., M. Arana & J. Streilein. 1994. Role of dermal cells from normal and ultraviolet B-damaged skin in induction of contact hypersensitivity and tolerance. Journal of Immunology 152:3317–3323.

Landsteiner, K. & J. Jacob. 1935. Studies on the sensitization of animals with simple chemical compounds. Journal of Experimental Medicine 61:643–656.

Maguire, J.H. 1995. Murine recombinant interleukin-12 increases the acquisition of allergic contact dermatitis in the mouse. International Archives of Allergy Immunology 106:166–168.

Manome, H., S. Aiba & H. Tagami. 1999. Simple chemicals can induce maturation and apoptosis of dendritic cells. Immunology 98:481–490.

Martin, T. & M. Bracken. 1986. Association of low birth weight and passive smoke exposure in pregnancy. American Journal of Epidemiology 124:633–642.

Mays, C.E., J.J. De Jongh & E.A. Hellmann. 1997. Genetic and environmental effects of sidestream smoke on pup survivorship of three inbred strains of mice. Proceedings of the Indiana Academy of Science 106:175–189.

Mays, C.E. & S.C. Mays. 1999. Immunosuppression of contact hypersensitivity by sidestream smoke in ICR mice. American Zoologist 39:73A.

Mosmann, T., H. Cherwinski, M. Bond, M. Giedlin & R. Coffman. 1986. Two types of helper T cell clones. I. Definition according to profiles of lymphokine activities and secreted proteins. Journal of Immunology 136:2348–2357.

Murayama, M., H. Yasuda, Y. Nishimura & M. Asahi. 1997. Suppression of mouse contact hypersensitivity after treatment with antibodies to leukocyte function-associated antigen-1 and intercellular adhesion molecule-1. Archives of Dermatology Research 289:98–103.

Nagai, H., Y. Ueda, T. Ochi, Y. Hirano, H. Tanaka, N. Inagaki & K. Kawada. 2000. Different role of IL-4 in the onset of hapten-induced contact hypersensitivity in BALB/c and C57BL/6 mice. British Journal of Pharmacology 129:299–306.

Niizeki, H. & J. Streilein. 1977. Hapten-specific tolerance induced by acute, low-dose ultraviolet B radiation of skin is mediated via interleukin-10. Journal of Investigative Dermatology 109: 25–30.

Nuriya, S., H. Yagita, K. Okumura & M. Azuma. 1996. The differential role of CD86 and CD80 costimulatory molecules in the induction and the effector phases of contact hypersensitivity. International Immunology 8:917–926.

Phanuphak, P., J.W. Moorhead & H.N. Claman. 1974. Tolerance and contact hypersensitivity to DNFB in mice. Journal of Immunology 112: 115–123.

Resnik, G. & G. Marquard. 1980. Effect of cigarette inhalation during pregnancy in Sprague-Dawley rats. Journal of Environmental and Pathological Toxicology 45:141–152.

Rhein, L., M. Haren & E. Bushler. 1993. Alterations in the cutaneous immune response following topical applications of sodium lauryl sulfate and kathon CG. Journal of Toxicology: Cutaneous and Ocular Toxicology 12:249–259.

Riemann, H., A. Schwarz, S. Grabbe, Y. Aragane, T.A. Luger, M. Wysoka, M. Kubin, G. Trinchieri & T. Schwarz. 1996. Neutralization of IL-12 in vivo prevents induction of contact hypersensitivity and incudes hapten-specific tolerance. Journal of Immunology 156:1799–1803.

Rissoan, M., V. Soumelis, N. Kadowaki, G. Grouard, F. Briere, R. Malefyt & J. Liu. 1999. Reciprocal control of T helper cell and dendritic cell differentiation. Science 283:1183–1186.

Ross, R., C. Gillitzer, R. Kleinz, J. Schwing, H. Kleinert, U. Foerstermann & A.B. Reske-Kunz. 1998. Involvement of NO in contact hypersensitivity. International Immunology 10:61–69.

Rowden, G., M. Lewis & A. Sullivan. 1977. Ia antigen expression in human epidermal Langerhans cells. Nature 268:247–248.

Sauder, D., K. Tamaki, A. Moshell, H. Fujiwara & S. Katz. 1981. Induction of tolerance to topically applied TNCB using TNP-conjugated ultraviolet light-*irradiated* epidermal cells. Journal of Immunology 127:261–265.

Schmitt, D.A., L. Owen-Schaub & S.E. Ullrich. 1995. Effect of IL-12 on immune suppression and suppressor cell induction by ultraviolet radiation. Journal of Immunology 153:5366–5372.

Schwarz, A., S. Grabbe, Y. Aragane, K. Sandkuhl, H. Riemann, T. Luger, M. Kubin, G. Trinchieri & T. Schwarz. 1996. Interleukin-12 prevents ultraviolet B-induced local immunosuppression and overcomes UVB-induced tolerance. Journal of Investigative Dermatology 106:1187–1191.

Schwarz, T. 1995. Interleukin-12 and its role in cutaneous sensitization. Research Immunology 146:494–498.

Shimada, S., S. Caughman, S. Sharrow, D. Stephany & S. Katz. 1987. Enhanced antigen-presenting capacity of cultured Langerhans cells in association with markedly increased expression of Ia antigen. Journal of Immunology 139:2551–2555.

Simkin, G.O., J.S. Tao, J.G. Levy & D.W. Hunt. 2000. IL-10 contributes to the inhibition of con-

tact hypersensitivity in mice treated with photodynamic therapy. Journal of Immunology 164: 2457–2462.

Simon, J., R. Tigelaar, P. Bergstresser, D. Edelbaum & P. Cruz, Jr. 1991. Ultraviolet B radiation converts Langerhans cells from immunogenic to tolerogenic antigen-presenting cells: Induction of specific clonal energy in $CD4^+$ T helper 1 cells. Journal of Immunology 146:486–491.

Smith, S.L., J.A. Martinson, J. Welter & J.E. Miripol. 1997. Irradiation of murine donor spleen cells with ultraviolet "B" light eliminates graft-versus host and host-versus-graft response in allogeneic recipient mice. In Vitro Cellular and Developmental Biology of Animals 33:674–676.

Tam, R.C., U.T. Phan, T. Milovanovic, B. Pai, C. Lim, Baird & L. He. 1997. Oligonucleotide mediated inhibition of CD28 expression induces human T cell hyporesponsiveness and manifests impaired contact hypersensitivity in mice. Journal of Immunology 158:200–208.

Tamaki, T., H. Fujiwara & S. Katz. 1981. The role of epidermal cells in the induction and suppression of contact hypersensitivity. Journal of Investigative Dermatology 76:275–278.

Tang, H.L. & J.G. Cyster. 1999. Chemokine upregulation and activated T cell attraction by maturing dendritic cells. Science 284:819–822.

Towes, G., P. Bergstresser & J. Streilein. 1980. Epidermal Langerhans cell density determines whether contact hypersensitivity or unresponsiveness follows skin painting with DNFB. Journal of Immunology 124:445–453.

Trinchieri, G. 1994. Interleukin-12 and its role in generation of Th-1 cells. Immunology Today 14: 335–337.

Ullrich, S.E. 1994. Mechanism involved in the systematic suppression of antigen-presenting cell function by UV irradiation. Journal of Immunology 152:3410–3416.

Unanue, E. 1984. Antigen-presenting function of the macrophage. Annual Review of Immunology 2:395.

U.S. Department of Health and Human Services. 1986. The health consequences of involuntary smoking. A report of the Surgeon General. Rockville, Maryland: U.S. Department of Health and Human Services, Public Health Service, Centers for Disease Control, Center for Health Promotion and Education, Office of Smoking and Health. DHHS Publication No. (CDC) 87-8398.

Wang, B., H. Fujisawa, L. Zhuang, S. Kondo, G. Shivji, C. Kim, T. Mak & D. Sauder. 1997. Depressed Langerhans cell migration and reduced contact hypersensitivity response in mice lacking TNF receptor p75. Journal of Immunology 159: 6148–6155.

Wang, H., N. Tedla, A. Lloyd, D. Wakefield & H. McNeil. 1998. Mast cell activation and migration to lymph nodes during induction of an immune response in mice. Journal of Clinical Investigation 102:1617–1626.

Weigmann, B., J. Schwing, H. Huber, R. Ross, H. Mossmann, J. Knop & A.B. Reske-Kunz. 1997. Diminished contact hypersensitivity response in IL-4 deficient mice at a late phase of the elicitation reaction. Scandinavian Journal of Immunology 45:308–314.

White, J.R. & H.F. Froeb. 1980. Small-airway dysfunction in nonsmokers chronically exposed to tobacco smoke. New England Journal of Medicine 302:720–723.

Wigle, D., N. Collishaw, J. Kirkbride & Y. Mao. 1987. Deaths in Canada from lung cancer due to involuntary smoking. Canadian Medical Association Journal 136:945–951.

Xu, H., A. Banerjee, N.A. DiIulio & R.L. Fairchild. 1997a. Development of effector $CD8^+$ T cells. Journal of Immunology 158:4721–4728.

Xu, H., P.S. Heeger & R.L. Fairchild. 1997b. Distinct roles for B7-1 and B7-2 determinants during priming of effector CD8 super (+) Tc1 and regulatory CD4 super (+) Th2 cells for contact hypersensitivy. Journal of Immunology 159: 4217–4226.

Xu, H., K. Aoyama, A. Kitani, S. Yu, T. Matsuyama & T. Matsushita. 1998. Interleukin-12 enhances contact hypersensitivity by modulating the in vivo cytokine pattern in mice. Journal of Interferon and Cytokine Research 18:23–31.

Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey. 663 pp.

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REASSESSMENT OF THE ALLEGHENY WOODRAT (*NEOTOMA MAGISTER*) IN INDIANA

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ABSTRACT. In the early 1980s, extant populations of the endangered Allegheny woodrat (*Neotoma magister*) in Indiana were reported from 20 sites (18 bluffs, 2 caves) adjacent to the Ohio River in Harrison and Crawford Counties. To assess the species' current status, live trapping surveys were conducted at 17 sites (access to the remaining three was denied) in 1991–1992. A total of 101 woodrats (50♂:51♀) was captured 144 times in 1551 trap-nights at 12 (11 bluffs, 1 cave) of the 17 sites. No woodrats were captured in Wyandotte Cave or on four bluffs in Crawford (n = 3) and Harrison (n = 1) Counties. Population declines were evident at four additional bluff sites. Existing populations were mostly limited to south-facing limestone cliffs bordering the Ohio River from Evans Landing in Harrison County downstream to Alton in Crawford County, the same range limits reported a decade earlier. To search for new populations, 41 sites in Clark, Crawford, Floyd, Harrison, Jefferson, Monroe, Orange and Perry Counties were inspected for woodrat activity in 1992–1993. Woodrats were found at only three sites (2 caves, 1 bluff) in Harrison County, which extended the species' known range in Indiana 2 km east along the Ohio River. Biennial monitoring of extant populations yielded 128 woodrats (54♂:74♀) at 14 sites in 1993–1994 and 123 woodrats (50♂:73♀) at 12 of 15 sites in 1996. Marked individuals comprised 9.4% and 10.6% of the total catch in 1993–1994 and 1996, respectively. Allegheny woodrats were most abundant on Bull's Point Bluff, Harrison-Crawford State Forest, and Rabbit Hash Ridge, which comprised >90% of the individuals taken in each biennial survey. Future conservation efforts should include periodic monitoring of extant sites and inspection of formerly-occupied sites, identification of factors limiting woodrat populations, and development of management recommendations for land owners and managers.

Keywords: Allegheny woodrat, conservation, distribution, Indiana, *Neotoma magister*, population, survey

The Allegheny woodrat (*Neotoma magister* Baird) inhabits cliffs, outcrops, talus slopes, caves, abandoned mines and other rocky habitats in deciduous forests of the eastern United States. *Neotoma magister* (= *N. pennsylvanica* Stone) was originally recognized as a distinct species (Goldman 1910) but was later reclassified as a subspecies of the eastern woodrat (*N. floridana* Ord; Burt & Barkalow 1942; Schwartz & Odum 1957). However, genetic and morphological studies (Hayes & Harrison 1992; Hayes & Richmond 1993) concluded *N. magister* warrants classification as a separate species. Historically, Allegheny woodrats occupied the Appalachian Mountain system from eastern New York southward to northern Alabama and west into Kentucky, Indiana and Tennessee (Poole 1940). Native populations have declined recently, particularly in the northeastern United States and the species has been extirpated from New York. Additionally, woodrats have restricted or reduced distributions in New Jersey, Pennsylvania, Maryland, Indiana and Ohio (Whitaker & Hamilton 1998). Causes for the declines are unclear; but potential factors include habitat fragmentation, increased predation, changes in forest composition, severe winter weather, infection from the parasitic raccoon roundworm (*Baylisascaris procyonis*), and decreased mast production due to gypsy moth (*Lymantria dispar*) invasion (see Balcom & Yahner 1996).

Allegheny woodrats have been listed as endangered in Indiana since 1984 and are limited to the unglaciated, south-central portion of the state. The species was first documented in 1930 from Harrison County (Hickie & Harrison 1930) although earlier accounts (e.g., Cope 1872) refer to what were probably woodrats in Wyandotte Cave in Crawford County. Cave deposits indicate woodrats once ranged as far north as Owen County (Richards 1972; 1986), but the species' modern range is restricted to the limestone escarpments that

border the Ohio River in extreme southern Indiana. Mumford (1975) found no evidence of woodrats in the Hoosier National Forest but reported three active colonies in Harrison and Crawford Counties. Similarly, Whitaker (1979) found no sign of woodrats at 109 sites in the Hoosier National Forest. Mumford & Whitaker (1982) list specimen records from Crawford and Harrison Counties and other records from five additional counties (Jennings, Lawrence, Monroe, Orange and Owen). Cudmore (1985) examined 100 sites in Clark, Crawford, Harrison, Jefferson, Perry, Spencer and Washington Counties but found evidence of extant populations at only 20 sites (18 bluffs, 2 caves) in Crawford and Harrison Counties. Four additional sites in Crawford and Harrison Counties had only old sign and were considered inactive.

Given population declines elsewhere, field surveys were conducted from 1991 through 1996 to reassess the status and distribution of the Allegheny woodrat in Indiana. The objectives were to determine the occurrence and relative abundance of woodrats at the 24 sites reported by Cudmore (1985), to assess population trends at occupied sites, and to search for new localities because rocky bluffs that appear suitable for woodrats are abundant along the Ohio River.

METHODS

Site selection and field searches.—The 24 sites reported by Cudmore (1985) were transcribed from topographic maps (1:24,000) at Indiana State University. Each site was visited to locate suitable rock features (e.g., overhangs, deep crevices and ledges) and to search for evidence of woodrats. Allegheny woodrats leave conspicuous sign such as fresh plant cuttings, hard mast caches, debris piles, nests and fecal deposits; consequently, their presence can often be determined by visual inspection. The rim, base, accessible tiers and any abandoned buildings were inspected at bluff sites. At caves, the entrance, twilight zone, adjacent outcrops and passages reported by previous researchers to have woodrat activity were examined.

Searches for new localities were conducted in 1992 and 1993. Potential sites were identified from topographic maps based on vertical relief and from reports of woodrat activity received from cavers. These sites were then inspected specifically for woodrat sign or while conducting other activities (i.e., bat hibernacula censuses). They were subsequently trapped only if fresh sign was found during initial searches.

Live trapping.—Single-door live traps (40.6 cm long, 12.7 cm wide, 12.7 cm high) baited with sliced apples were used to capture woodrats. To reduce disturbance during the peak reproductive period (i.e., April and May; Cudmore 1983), trapping was conducted from June through October. The 20 sites reported occupied by Cudmore (1985) were surveyed in October 1991 and from June through October 1992. At each bluff site, 25–59 traps ($\bar{x}$ = 42.1) were set for two consecutive nights ($\bar{x}$ trap-nights per site = 84.2; SD = 23.0). The single exception was Cold Friday Hollow Bluff (site #75), which was surveyed in two sessions due to its length (>1500 m), abundance of optimal habitat, and fresh woodrat sign. Trap effort at the two caves ($\bar{x}$ = 60.0 trap-nights; SD = 14.1) depended on passage length and complexity, presence of woodrat sign and availability of rock outcrops near the entrance. At all sites, traps were placed near activity areas (e.g., latrines, food caches, nests) and throughout suitable habitat found during initial searches. Traps were set in late afternoon, checked early the following morning, and checked and removed on the second morning. Sex, age class, body weight (to nearest 2.5 g) and reproductive status were noted for each woodrat. A numbered Monel size #1 tag was placed in each ear. Unless reproductive status indicated otherwise, pelage coloration and body weights (Mengak 1991) were used to assign age class (i.e., juveniles: <175 g; subadult: 175–224 g; adult: ≥225 g).

Biennial monitoring program.—Once extant colonies were identified, either at new or previously-known sites, population trends were assessed by a biennial monitoring program. Occupied sites were live trapped in 1993–1994 and 1996 using standard survey protocol (i.e., *ca.* 40 traps for two consecutive nights). Traps were again placed near activity areas or at previous capture sites to assess site fidelity and survival. Captured woodrats were processed as previously described and released immediately after handling.

RESULTS

Surveys of sites occupied in 1980–1983.—Landowners granted permission to trap 17 (15

bluffs, 2 caves) of the 20 sites occupied by woodrats in the early 1980s. Average length of bluff surveyed was 928 ± 473 m. From October 1991 through October 1992, 101 woodrats (50♂:51♀) were captured 144 times in 1551 trap-nights at 12 (11 bluffs, 1 cave; Table 1) of 17 sites. Mean capture rate at occupied sites was 8.5 individuals/100 trap-nights (range: 1.2–26.8). Distribution by sex and age class was 32 adult ♂, 32 adult ♀, 6 subadult ♂, 12 subadult ♀, 11 juvenile ♂, and 7 juvenile ♀. Age of one male was not determined. An average of 8.4 woodrats was captured at occupied sites (range: 1–26), but only 6 sites yielded ≥5 animals. Evidence of reproduction at 10 sites included juvenile woodrats (6 sites), late-season subadults (2 sites), pregnant females (1 site) and a scrotal male (1 site). Latest capture dates for juveniles, lactating females and scrotal males were 24 September, 22 July and 25 October, respectively. Relative abundance at 10 occupied bluffs ranged from 2.5–25.0 woodrats/km of bluff ($\bar{x}$ = 11.1, SD = 7.8). These are minimal values because it is unlikely all resident woodrats were captured and populations may be greater at sites surveyed later in the season due to annual recruitment.

Eleven of 12 occupied sites were associated with extensive limestone bluff systems bordering the Ohio River (Fig. 1) from Evans Landing in Harrison County downstream to Alton in Crawford County (*ca.* 74 river km), the same range limits reported by Cudmore (1985). The other site, Potato Run Cave, was in Harrison-Crawford State Forest (HCSF) about 1.2 km from occupied bluff habitat. Only one confirmed site (Bull's Point Bluff) was in Crawford County; the remaining 11 were in Harrison County.

No woodrats were captured at five sites including Scenic View Bluff in Harrison County and Leavenworth Bluff, Lowe/Booth Bluff, South Fredonia Bluff and Wyandotte Cave in Crawford County (Table 1; Fig. 1). Suitable rock overhangs, crevices and ledges were common at several of these bluff sites; but no fresh sign or other recent evidence of woodrats was found. Access was denied to the three remaining sites (2 bluffs, 1 abandoned building) occupied by woodrats in the early 1980s. A cursory search of Mulzer #8 and Mulzer #97 bluffs near Mauckport revealed suitable rock features and old sign but no evidence of an extant population. The abandoned building (site #83) on privately-owned Nye Bluff lies between two occupied bluff sites on HCSF but was not visited.

The four sites (3 bluffs, 1 abandoned building) considered inactive by Cudmore (1985) were also searched to assess if woodrats had recolonized the sites (Table 1). However, no sign was found at Wildcat Cave and Mauckport Cemetery bluffs while Indian Hollow Bluff yielded only old sign (i.e., disheveled nest and food cache). The abandoned building on the Blue River at site #48 had been destroyed, and the surrounding habitat was unsuitable for woodrats. These four sites were not trapped during the study.

Searches for new localities.—From May 1992 through September 1993, 41 sites in Clark, Crawford, Floyd, Harrison, Jefferson, Monroe, Orange and Perry Counties were searched for evidence of woodrats. Most sites (n = 26; 68%) were associated with limestone outcrops or bluff systems along the Ohio River (Fig. 2) and averaged 879 ± 291 m in length. Nine caves were inspected, primarily during bat hibernacula censuses in January 1993. Two sites in the Hoosier National Forest, Derby Cemetery and Buzzard's Roost bluffs, had been examined previously by Whitaker (1979) while eight other bluff sites had been visited by Cudmore (1985).

Allegheny woodrats were confirmed at only three of 41 sites, all in Harrison County (Table 2). Two were small caves in HCSF ≤2.5 km of occupied bluffs on the Ohio River. Only one woodrat was captured in each cave during limited trapping sessions (i.e., 8–10 trap-nights per cave) in October 1992. The third locality, Noes Park Bluff (site #134), extended the known range of Allegheny woodrats about 2 km east from Rabbit Hash Ridge (Fig. 2). Seven woodrats, including 5 adults, 1 subadult, and 1 juvenile were captured at Noes Park Bluff in August 1993.

Evidence of former occupancy (e.g., old latrines, food caches, nests) was found at eight sites in Harrison (n = 4), Crawford (n = 3) and Monroe (n = 1) Counties (Table 2). Most (63%) were caves, which probably provided better conditions for preserving woodrat sign than those on exposed bluff sites. Although many bluffs had suitable overhangs, crevices and ledges, old sign was found only at Angelwing Arch (Crawford County) and Moore

Table 1.—Results of live trapping surveys for Allegheny woodrats at active (n = 20) and inactive (n = 4) sites reported by Cudmore (1985) in Crawford and Harrison Counties, Indiana, September 1991–October 1992. Previous status reported by Cudmore (1985): A = active; I = inactive. Ownership: HCSF = Harrison-Crawford State Forest; p = private. Relative abundance expressed as number of woodrats/km of bluff; estimates not provided for caves or bluff sites at which no woodrats were captured.

Site no.	Site name	Previous status	Ownership	Survey dates	Trap-nights	No. woodrats	Adults	Subadults & juveniles	Relative abundance
Crawford County									
10	Wyandotte Cave	A	HCSF	16–18 Oct 1991	70	0	0	0	—
14	Leavenworth Bluff	A	p	25–27 Aug 1992	116	0	0	0	—
15	Indian Hollow Bluff	I	HCSF	28 Sep 1992		old sign found; site not trapped			
30	Lowe/Booth Bluff	A	p	14–16 Sep 1992	98	0	0	0	—
36	South Fredonia Bluff	A	p	21–23 Oct 1992	46	0	0	0	—
39	Bull's Point Bluff	A	p	13–15 Oct 1992	102	7	3	4	3.7
40	Wildcat Cave Bluff	I	HCSF	12 Sep 1991		no sign found; site not trapped			
Harrison County									
1	Tobacco Landing	A	p	28–30 Jul 1992	116	2	0	2	2.5
2	Shelterhouse #2 Bluff	A	HCSF	2–4 Oct 1991	82	22	15	6	25.0
4	Scenic View Bluff	A	p	12–14 Aug 1992	70	0	0	0	—
7	Mauckport Cemetery Bluff	I	p	5 Aug 1992		no sign found; site not trapped			
8	Mulzer #8 Bluff	A	p	17 Aug 1992		old sign found; site not trapped (access denied)			
17	Potato Run Cave	A	HCSF	16–18 Oct 1991	50	1	1	0	—
19	Rabbit Hash Ridge - U	A	p	22–24 Jun 1992	55	8	4	4	10.4
20	Rabbit Hash Ridge - C	A	p	22–24 Jun 1992	62	2	2	0	4.8
21	Rabbit Hash Ridge - D	A	p	30 Jun–2 Jul 1992	76	10	7	3	18.3
47	The Narrows Bluff	A	p	20–22 Jul 1992	74	4	3	1	5.5
48	Blue River Building	I	HSCF	11 Sep 1991		building destroyed; surrounding habitat unsuitable			
75	Cold Friday Hollow Bluff	A	HCSF	9–11, 22–24 Sep 1992	252	26	17	9	16.7
81	Overflow Pond Bluff	A	p	1–3 Jun 1992	82	1	1	0	—
82	South HCSF Bluff	A	HCSF	8–10 Jun 1992	118	14	7	7	17.7
83	Nye Building	A	p			site not visited (access denied)			
97	Mulzer #97 Bluff	A	p	17 Aug 1992		old sign found; site not trapped (access denied)			
98	South Nye Bluff	A	HCSF	23–25 Oct 1991	82	4	4	0	6.0
	Total all sites				1551	101	64	36	11.1

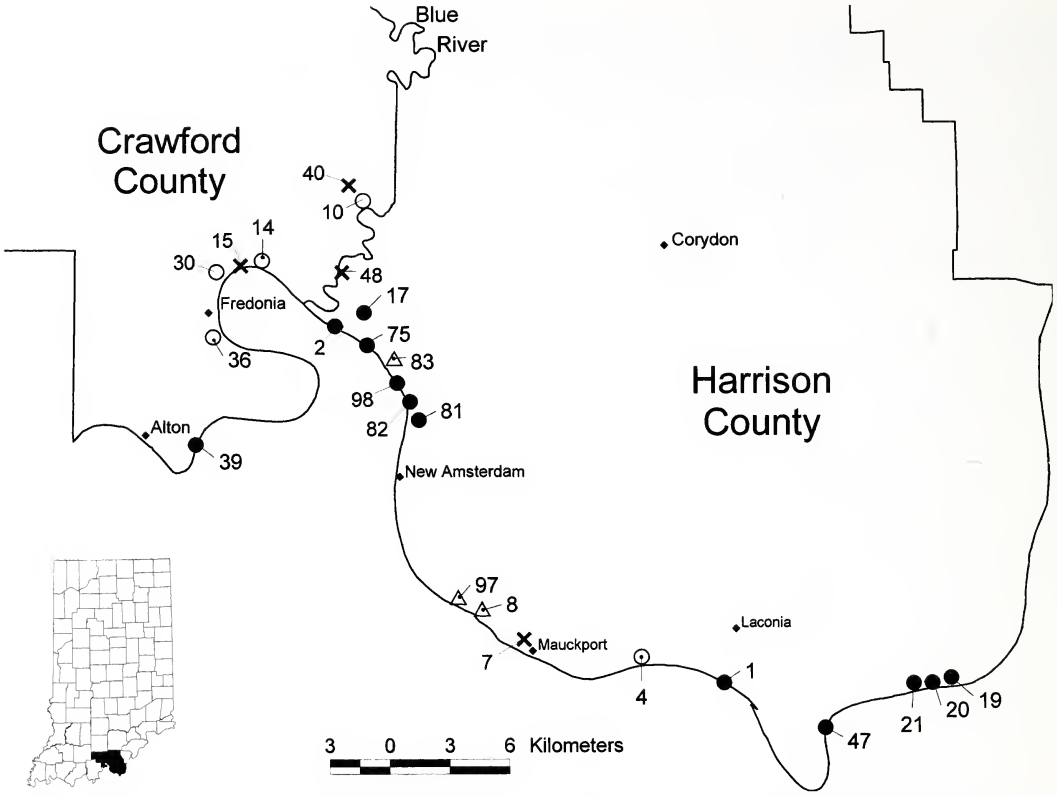

Figure 1.—Results of live trapping surveys at 20 active sites for Allegheny woodrats reported by Cudmore (1985) in Crawford and Harrison Counties, Indiana, September 1991–October 1992. Solid circles (●) denote sites occupied by woodrats (n = 12); open circles (○) denote sites at which no woodrats were captured (n = 5); open triangles (△) denote sites to which access was denied (n = 3). Crosses (×) denote inactive sites (n = 4) reported by Cudmore (1985).

Chapel Bluff and North New Amsterdam Bluff in Harrison County.

Biennial monitoring of extant sites.—In September–October 1993 and June–October 1994, 128 woodrats (54♂:74♀) were captured 216 times in 1136 trap-nights at 14 sites (11 bluffs, 3 caves) that were occupied in 1991–1992. This represents a 24% increase over the number of animals taken in 1991–1992, largely due to gains at bluff sites #39, #82 and #98 (Fig. 3). There was relatively little change noted at the remaining 11 sites. Twelve (6♀:6♂) of 128 woodrats (9.4%) were recaptures first taken in 1991–1992 as juveniles (n = 2), subadults (n = 5) or adults (n = 4). The identity of one adult male was unknown because both ear tags had been lost. Elapsed time between recapture dates ranged from 16–26 months ($\bar{x}$ = 22.8). Ten woodrats were recaptured at their original sites including six individuals (2♂:4♀) taken ≤10 m from their initial trap location. Three other woodrats (2♂:1♀), all juveniles or subadults in 1992, were recaptured two years later 45–255 m ($\bar{x}$ = 140) from their first capture site. A subadult male caught in June 1992 on site #82 was recaptured in October 1993 at site #98, about 1.2 km from his initial capture site.

From July–October 1996, 123 woodrats (50♂:73♀) were captured 206 times in 1207 trap-nights at 12 (11 bluffs, 1 cave) of 15 sites. This represents a 9% decline in the number taken in 1993–1994. No woodrats were captured at Overflow Pond Bluff, P.P. Pot Cave and Limekiln Hollow Cave. Few animals (≤3) were captured here previously, and only a single adult was caught in either cave in 1992 and 1994. Also, marked declines were evident at bluff sites #82 (−48%) and #98 (−55%) in HCSF (Fig. 3). Compared to

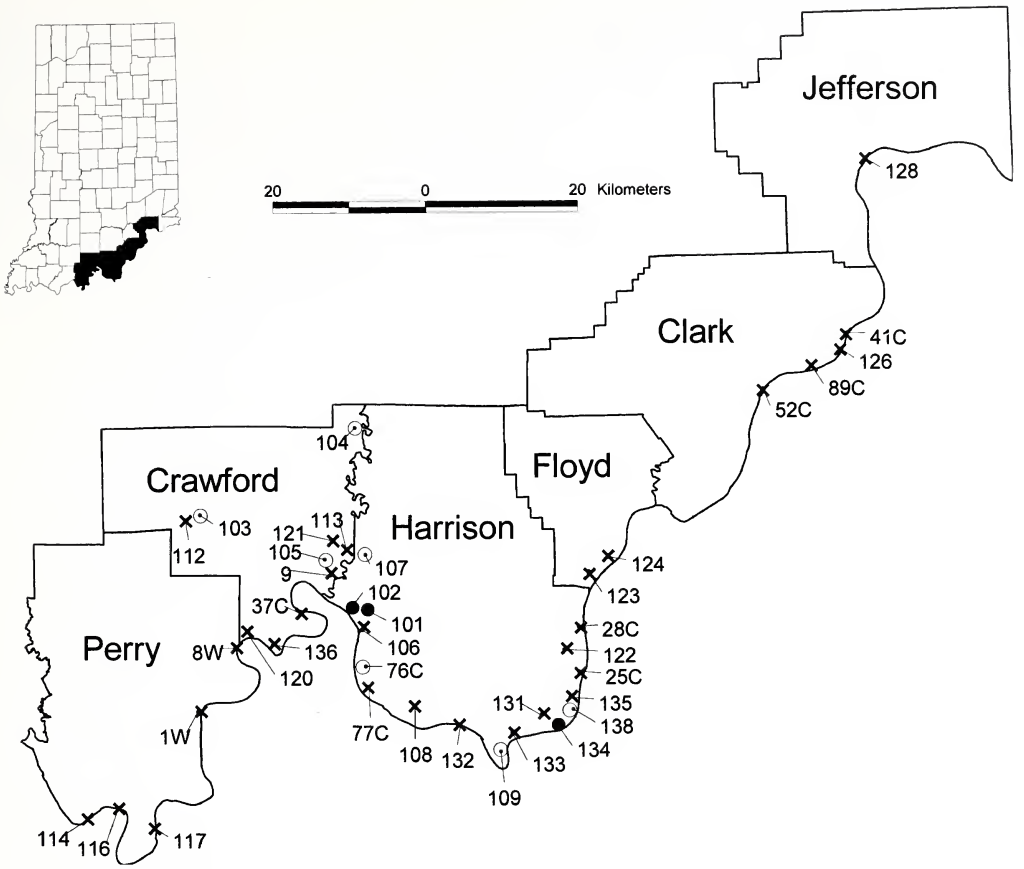

Figure 2.—Distribution of sites (n = 39) inspected for Allegheny woodrats in Clark, Crawford, Floyd, Harrison, Jefferson and Perry Counties, Indiana, May 1992–September 1993. Solid circles (●) denote sites at which woodrats were found (n = 3); open circles (○) denote sites at which old sign was found (n = 7); crosses (×) denote sites at which no sign was found (n = 29). Sites #110 (Saltpeter Cave, Monroe County) and #111 (Elrod Gulf, Orange County) not shown.

1993–1994, eight sites yielded 1–10 ($\bar{x}$ = 3.5) fewer woodrats; but five other sites yielded 1–7 ($\bar{x}$ = 3.2) more woodrats. Thirty-two woodrats were captured at Bull's Point Bluff (site #39), nearly a five-fold increase since 1992 and the greatest number taken during this study. Thirteen (3♂:10♀) of 123 woodrats (10.6%) were recaptures first taken in 1993–1994 as juveniles (n = 1), subadults (n = 2) or adults (n = 8). The identity of two males was unknown because they had lost their ear tags. The remaining 11 were recaptured at their original sites including eight individuals (1♂:7♀) taken ≤5 m from their initial capture site. Elapsed time between recapture dates for these 11 woodrats ranged from 22–37 months ($\bar{x}$ = 25.0).

DISCUSSION

Allegheny woodrats were found at 12 of 17 (71%) sites occupied over a decade ago and have essentially the same distribution as reported by Cudmore (1985). However, their occurrence within this range is disjunct, likely due to the availability of complex cliffs that provide suitable fissures and crevices for cover and nest sites. Fresh sign (e.g., latrines, green cuttings) was evident at occupied sites, and its presence was a reliable indicator of an extant population. Failure to capture woodrats at five recently-occupied sites, however, may not provide conclusive evidence of a local extinction. Portions of bluff sites were inaccessible for field searches or live trapping. Fur-

Table 2.—Results of field searches for new localities for Allegheny woodrats at 41 sites in Clark, Crawford, Floyd, Harrison, Jefferson, Monroe, Orange, and Perry Counties, Indiana, May 1992–September 1993. Sites with C (n = 8) denote those visited by Cudmore (1985); sites with W (n = 2) denote those visited by Whitaker (1979). Ownership: DNP = Division of Nature Preserves; HCSF = Harrison-Crawford State Forest; HNF = Hoosier National Forest; TNC = The Nature Conservancy; p = private.

Site no.	Site name	County	Ownership	Search period	Results
41C	Blue Ridge Bluff	Clark	p	Jul 1993	no sign
52C	Devil's Backbone	Clark	p	Jul 1993	no sign
89C	Bull Creek Bluff	Clark	p	Jul 1993	no sign
126	Bull Creek Cemetery Bluff	Clark	p	Jul 1993	no sign
9	Wyandotte Lake Bluff	Crawford	HCSF	Jan 1993	no sign
31	Saltpeter Cave	Crawford	HCSF	Jan 1993	no sign
37C	Artist's Point Bluff	Crawford	p	Sep 1993	no sign
103	Angelwing Arch	Crawford	HNF	Oct 1992	old sign
104	Robinson's Ladder Cave	Crawford	p	Jan 1993	old sign
105	Turtle Cave	Crawford	HCSF	Jan 1993	old sign
112	Hemlock Cliffs	Crawford	HNF	Oct 1992	no sign
120	Section 31 Bluff	Crawford	HNF	Jul 1993	no sign
121	Little Wildcat Cave	Crawford	HCSF	Jun 1993	no sign
136	Little Blue River Bluff	Crawford	p	Aug 1993	no sign
123	Brock-Sampson Glade	Floyd	DNP	Jun 1993	no sign
124	Gap Hollow Bluff	Floyd	p	Jun 1993	no sign
25C	Fishtown Bluff	Harrison	p	Jun 1993	no sign
28C	Blunk Point Bluff	Harrison	p	Jun 1993	no sign
76C	North New Amsterdam Bluff	Harrison	p	Jul 1993	old sign; no woodrats captured in Aug 1996
77C	South New Amsterdam Bluff	Harrison	p	Jul 1993	no sign
101	P. P. Pot Cave	Harrison	HCSF	May 1992	fresh sign; 1 woodrat captured in Oct 1992
102	Limekiln Hollow Caves	Harrison	HCSF	May 1992	fresh sign; 1 woodrat captured in Oct 1992
106	Cold Friday Hollow Karst	Harrison	HCSF	Oct 1992	no sign
107	Formation Pit Cave	Harrison	HCSF	May 1992	old sign
108	Scenic View Overlook Bluff	Harrison	county	not specified	no sign
109	Wallier Cave	Harrison	p	Aug 1992	old sign
122	Stoner Hill Bluff	Harrison	TNC	Aug 1993	no sign
131	Teeple Glade	Harrison	TNC	Jun 1993	no sign

Table 2.—Continued.

Site no.	Site name	County	Ownership	Search period	Results
132	Mile 643 Bluff	Harrison	p	Jul 1993	no sign
133	Mosquito Creek Bluff	Harrison	p	Aug 1993	no sign
134	Noes Park Bluff	Harrison	p	Jul 1993	fresh sign; 7 woodrats captured in Aug 1993
135	Rosewood Bluff	Harrison	p	Jul 1993	no sign
138	Moore Chapel Bluff	Harrison	p	Sep 1993	old sign
128	Devil's Backbone - Madison	Jefferson	p	Sep 1993	no sign
110	Saltpeter Cave	Monroe	p	Jan 1993	old sign
111	Elrod Gulf	Orange	p	not specified	no sign
1W	Derby Cemetery Bluff	Perry	p	Jul 1993	no sign
8W	Buzzard Roost Bluff	Perry	HNF	Jul 1993	no sign
114	Cannelton Bluff	Perry	HNF	Jun 1993	no sign
116	Dodd Bluff	Perry	p	Jul 1993	no sign
117	Adams/Sample Bluff	Perry	p	Jul 1993	no sign

ther, traps were set for only two consecutive nights and some resident woodrats may have avoided capture. To illustrate, 31 of 75 (41%) individuals taken on the second trap night in 1991–1992 were new captures. Nonetheless, Allegheny woodrats appear to have been extirpated from at least two sites. The abandoned building at site #36 was destroyed, and no sign or woodrats were found in the cliffs below the foundation. No evidence of woodrats was found in Wyandotte Cave (site #10), which is >6 km disjunct from established populations on the Ohio River. Hickie & Harrison (1930) and Lyon (1936) were unable to find woodrat sign in Wyandotte Cave, but *Neotoma* tracks were observed >500 m from the entrance in 1973 (Mumford & Whitaker 1982). We found no sign in areas of the cave reported to have woodrat activity, and personnel at Wyandotte Cave were unaware of any food caches, latrines or nests. Several of our traps were sprung or had chewed bait, which suggests *Peromyscus* spp. were present.

Cudmore (1985) reported an overall abundance of 27.5 woodrats/km of cliff, over twice that found in 1991–1992 (11.1 woodrats/km). Despite differences in survey protocol, population declines were apparent at 4 of 5 sites (Table 3). Lowe/Booth Bluff, where Cudmore (1985) captured 22 animals and found 12 active dens, yielded no woodrats and only old sign. Marked declines were also evident at Tobacco Landing, South HCSF Bluff and South Nye Bluff. In contrast, the population at Shelterhouse #2 increased from its previous level.

The original site boundaries established by Cudmore (1985) were maintained for consistency; but recapture data suggest regular movement between adjacent sites, particularly in HCSF and at Rabbit Hash Ridge. A subadult male from South HCSF Bluff was recaptured 16 months later on adjacent South Nye Bluff, about 1.2 km from his initial capture site. A subadult female caught on South HCSF Bluff in August 1994 was recaptured one month later on Cold Friday Hollow Bluff, nearly 3 km from her initial trap site. On Rabbit Hash Ridge, five woodrats (4 adult ♂, 1 subadult ♀) were recaptured within three weeks on adjacent sites 80–960 m ($\bar{x}$ = 450 m) from their initial trap site including an adult male that had moved 960 m overnight.

In Indiana, Allegheny woodrats were most abundant on Harrison-Crawford State Forest,

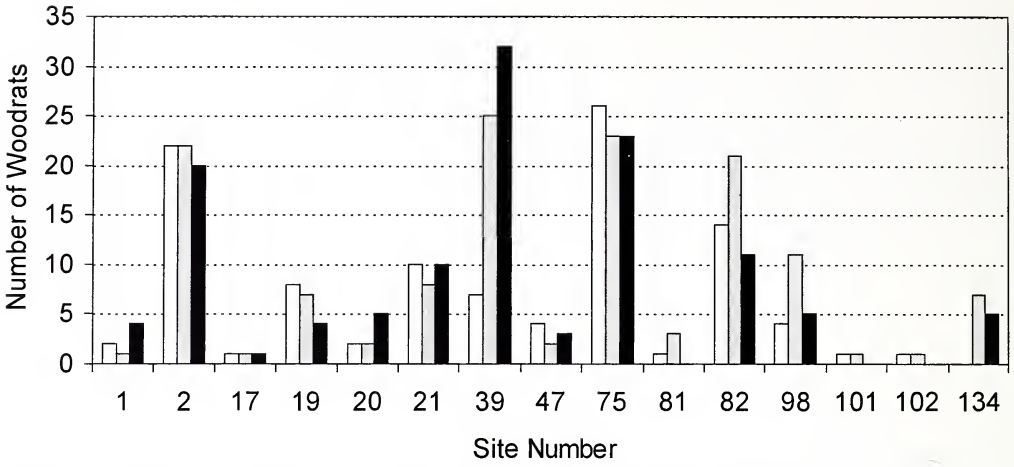

Figure 3.—Number of Allegheny woodrats captured during 1991–1992 (open bar), 1993–1994 (shaded bar) and 1996 (solid bar) surveys at 15 sites in Crawford and Harrison Counties, Indiana. Site #134 was not trapped in 1991–1992. No woodrats were captured in 1996 at sites #81, #101 and #102.

Rabbit Hash Ridge and Bull's Point Bluff. These three complexes support relatively large populations that accounted for >90% of the woodrats captured in 1991–1992, 1993–1994 and 1996. Population declines at individual sites within these complexes may be ameliorated by immigration of woodrats from adjacent, occupied habitats. For example, movement among the three contiguous sites on Rabbit Hash Ridge was common; and when treated as a unit, the total population remained relatively small yet stable (i.e., 20 woodrats in 1992, 17 in 1994 and 19 in 1996). Additional opportunities for interchange may be available from Noes Park Bluff (site #134), which is <2 km from Rabbit Hash Ridge. In contrast, the long-term viability of other sites (e.g., The Narrows, Tobacco Landing) is suspect because habitats were marginal or sites were spatially isolated from larger populations. Without immigration of dispersing woodrats from nearby sites, small localized populations may be more vulnerable to extirpation. Similarly, the three sites at which no woodrats were captured in 1996 (i.e., Overflow Pond Bluff, P.P. Pot Cave, Limekiln Hollow Cave) had few crevices and fissures or were disjunct from established bluff populations. Overflow Pond Bluff is probably periodically used by woodrats from adjacent cliffs in HCSF. However, P.P. Pot and Limekiln Hollow caves can support few animals because they are small, and adult woodrats are generally intolerant of one another (Wiley 1980).

Richards (1986) found fossil evidence of Allegheny woodrats throughout Indiana's karst region as far north as Owen and Shelby Counties, *ca.* 145 km north of present range and suggested indirect effects of climatic change (e.g., extended snow cover, availability of winter foods) caused the ancient depopulation. Marginal habitats such as small, wet caves and discontinuous rock outcrops with few crevices dominated most of this historic range. While prolonged factors such as climatic change may have caused a dramatic, long-term range reduction, woodrats have been extirpated or, at least, greatly reduced in <15 years from optimal habitats (i.e., south-facing limestone bluffs) within their current distribution. Balcom & Yahner (1996) found more residential, cropland and other agricultural cover at historic than occupied sites in Pennsylvania and claimed these land uses favored higher populations of ubiquitous predators such as great horned owls (*Bubo virginianus*) and raccoons (*Procyon lotor*). Both species have been implicated in woodrat declines in the northeast United States from increased predation or exposure to *Baylisascaris procyonis* (Balcom 1994; Balcom & Yahner 1996; McGowan 1993). In 1996, an adult female woodrat from Shelterhouse #2 in HCSF was found infected with raccoon roundworm

Table 3.—Number of Allegheny woodrats captured, capture rate, and relative abundance in 1980–1983 (Cudmore 1985) and 1991–1992 (this study) at 6 bluff sites in Crawford and Harrison Counties, Indiana. Capture rate expressed as number of individuals/100 trap-nights. Relative abundance expressed as number of woodrats/km of bluff. [1] Forty-four traps set for 3 consecutive nights and for 2 additional nights one week later. [2] At 5 sites listed above, 40–59 traps ($\bar{x}$ = 49.7) set for 2 consecutive nights.

Site no.	Site name	1980–1983 Survey[1]			1991–1992 Survey[2]		
		No. woodrats	Capture rate	Relative abundance	No. woodrats	Capture rate	Relative abundance
1	Tobacco Landing	15	30.6	16.1	2	1.7	2.5
2	Shelterhouse #2 Bluff	12	17.4	15.4	22	26.8	25.0
8	Mulzer #8 Bluff	4	5.5	8.3	site not trapped (access denied)		
30	Lowe/Booth Bluff	22	20.2	15.0	0	0.0	—
82	South HCSF Bluff	41	50.5	71.9	14	11.9	17.7
98	South Nye Bluff	21	28.2	38.5	4	4.9	6.0

larvae. It exhibited clinical neurologic disease; and eight *B. procyonis* larvae were recovered including one from the brain, four from the anterior carcass and three from the posterior carcass (K.R. Kazacos pers. comm.). *Baylisascaris procyonis* is transmitted from eggs shed in raccoon feces and is fatal to a wide range of secondary hosts (Kazacos & Boyce 1989). Woodrats may be particularly susceptible to infection because of their caching behavior, which includes raccoon feces (pers. obs.); but the prevalence of *B. procyonis* in woodrat habitat and its potential role in population declines in Indiana are unknown.

Future conservation efforts for Allegheny woodrats in Indiana should focus on identification of factors limiting extant populations (e.g., habitat fragmentation, raccoon roundworm infection, increased predation, changes in forest composition, availability of hard mast) and development of effective management strategies. With few exceptions, the biennial monitoring program initiated in this study detected relatively little change in woodrat populations at individual sites over a six-year period. Consequently, a less frequent monitoring schedule (e.g., 4–5 years) could be adopted at extant sites to determine species' presence and to monitor natural population fluctuations. Previously-occupied sites should be inspected periodically for fresh sign to determine if woodrats have recolonized former habitats.

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LITERATURE CITED

Balcom, B.J. 1994. Microhabitat and landscape characteristics associated with Allegheny wood-

rat (*Neotoma magister*) sites in Pennsylvania. M.S. thesis, The Pennsylvania State University, University Park. 109 pp.

Balcom, B.J. & R.H. Yahner. 1996. Microhabitat and landscape characteristics associated with the threatened Allegheny woodrat. Conservation Biology 10:515–525.

Burt, W.H. & F.S. Barkalow, Jr. 1942. A comparative study of the bacula of woodrats (subfamily Neotominae). Journal of Mammalogy 23:287–297.

Cope, E.D. 1872. Observations on Wyandotte Cave and its fauna. American Naturalist 6:406–422.

Cudmore, W.W. 1983. The distribution and ecology of the eastern woodrat, *Neotoma floridana*, in Indiana. Ph.D. dissertation, Indiana State University, Terre Haute. 148 pp.

Cudmore, W.W. 1985. The present distribution and status of the eastern woodrat, *Neotoma floridana*, in Indiana. Proceedings of the Indiana Academy of Science 94:621–627.

Goldman, E.A. 1910. Revision of the wood rats of the genus *Neotoma*. North American Fauna 31: 1–124.

Hayes, J.P. & R.G. Harrison. 1992. Variation in mitochondrial DNA and the biogeographic history of woodrats (*Neotoma*) of the eastern United States. Systematic Biology 41:331–344.

Hayes, J.P. & M.E. Richmond. 1993. Clinal variation and morphology of woodrats (*Neotoma*) of the eastern United States. Journal of Mammalogy 74:204–216.

Hickie, P.F. & T. Harrison. 1930. The Allegheny woodrat in Indiana. American Midland Naturalist 12:169–174.

Kazacos, K.R. & W.M. Boyce. 1989. *Baylisascaris* larva migrans. Journal of the American Veterinary Medical Association 195:894–903.

Lyon, M.W., Jr. 1936. Mammals of Indiana. American Midland Naturalist 17:1–384.

McGowan, E.M. 1993. Experimental release and fate study of the Allegheny woodrat (*Neotoma magister*). Federal Aid Project No. W-166-E-1, Delmar, New York. 15 pp.

Mengak, M.T. 1991. Woodrat investigations: population status and monitoring. Federal Aid Project EW-2-3-1, Richmond, Virginia. 14 pp.

Mumford, R.E. 1975. The status of the Indiana bat (*Myotis sodalis*) and the eastern woodrat (*Neotoma floridana*) on the Wayne-Hoosier National Forest, Indiana. *In* Distributional Studies of the Indiana Bat (*Myotis sodalis*) on Three National Forests of the Eastern Region. Final report, Eastern Region, U.S. Forest Service. 64 pp.

Mumford, R.E. & J.O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press, Bloomington, Indiana. 537 pp.

Poole, E.L. 1940. A life history sketch of the Allegheny woodrat. Journal of Mammalogy 21: 249–270.

Richards, R.L. 1972. The woodrat in Indiana: recent fossils. Proceedings of the Indiana Academy of Science 81:370–375.

Richards, R.L. 1986. The Quaternary distribution of the eastern woodrat, *Neotoma floridana*, in Indiana. Proceedings of the Indiana Academy of Science 96:513–521.

Schwartz, A. & E.P. Odum. 1957. The woodrats of the eastern United States. Journal of Mammalogy 38:197–206.

Whitaker, J.O., Jr. 1979. Studies of the eastern woodrat, *Neotoma floridana*, in the Hoosier National Forest, southern Indiana. Final report, Indiana State University, Terre Haute. 19 pp.

Whitaker, J.O., Jr. & W.J. Hamilton, Jr. 1998. Mammals of the Eastern United States. Cornell University Press, Ithaca, New York. 583 pp.

Wiley, R.W. 1980. *Neotoma floridana*. Mammalian Species No. 139. 7 pp.

Manuscript received 18 May 2001, revised 19 October 2001.

2002. Proceedings of the Indiana Academy of Science 1:67–76

A STUDY OF THE FROG LUNG FLUKE *HAEMATOLOECHUS* (TREMATODA: HAEMATOLOECHIDAE) COLLECTED FROM AREAS OF KENTUCKY AND INDIANA

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ABSTRACT. One hundred seventy-six frogs and toads collected from areas of the Ohio River Valley region of Kentucky and Indiana were examined for the presence of lung flukes (*Haematolechus* spp.). Of the six recognized species of *Haematolechus* in North America, four were identified from the frogs examined in this study. The following species of lung flukes were recovered: 412 *H. complexus*, 63 *H. longiplexus*, 23 *H. breviplexus* and 8 *H. varioplexus*. Prevalence of infected frog species was 54% *Rana utricularia*, 42% *R. clamitans*, 38% *R. catesbeiana*. The mean number of lung flukes per infected frog species was as follows: *R. utricularia*, 13.6; *R. clamitans*, 8.9; *R. catesbeiana*, 6.3. The highest intensity was 71 mature *H. complexus* in one *R. clamitans* specimen. The overall prevalence and intensity of lung flukes were significantly higher in male frogs than in female frogs. There was no significant difference in prevalence or intensity of lung flukes with regard to right or left lung. Two of the four *Haematoloechus* species (*H. complexus* and *H. varioplexus*) have not been reported from Kentucky or Indiana. These records constitute a new geographical distribution for these two parasite species. Additionally, unusual variations in sucker sizes of *H. longiplexus* are reported. The surface topography of a representative specimen of *H. complexus* was studied by scanning electron microscopy. Almost the entire body of the fluke was covered by flattened conical-shaped spines. However, the spines around the periphery of the genital pore and the rim of the oral sucker were sharply-attenuated. No sensory papillae were noted, and the entire tegument had a porous spongy structure, which may function in secretion.

Keywords: Trematoda, *Haematoloechus*, frog, lung fluke

Trematodes from the lungs of Anura were first reported over 200 years ago by Goeze (1782), who recognized a lung fluke in a frog and called it *Planaria cylindrica*. Rudolphi (1819) described a lung fluke from *Rana esculenta* and named it *Distomum variegatum*. This fluke was also studied and described as *Monostoma bombynae* by Zeder (1800) because he failed to see the ventral sucker. Looss (1894) described *M. bombynae* and later (1899) proposed a separate genus, *Haematoloechus*, for the frog lung fluke. Because of Stäl's hemipteran genus *Haematoloecha* established in 1874, Looss (1902) emended the genus *Haematoloechus* to *Pneumonoeces*. Harwood (1932) and Ingles (1932) independently pointed out that the name first chosen by Looss for this genus was not invalidated and should stand in accordance with International Code of Zoological Nomenclature. Although some authors have retained *Pneumonoeces*, *Haematoloechus* is widely accepted today.

A large number of amphibian helminth surveys have been published in North America. Early compilations included Stiles & Hassall (1894) and Pratt (1900). The first comprehensive systematic accounts were those of Stafford (1902a,b, 1905). Later studies on amphibian helminths from the United States include those by Cort (1915), Harwood (1932), Ingles (1936) and Manter (1938). Extensive work has also been done in Oklahoma (Kuntz & Self 1944), Iowa (Ulmer 1970) and Nebraska (Brooks 1976). More recent surveys have been conducted in Michigan (Muzzall 1991), Illinois (Andrews et al. 1992) and Arizona (Goldberg et al. 1998).

Our present knowledge of trematode parasites of amphibians from Indiana and Kentucky is scarce. Cort (1915) reported finding the lung flukes *H. longiplexus* and *H. breviplexus* from North Judson, Indiana. Krull (1931) also found *H. longiplexus* in a bullfrog

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from Indiana. Also, Lank (1971) found *H. longiplexus* and *H. breviplexus* in Indiana.

Several species of flukes have been studied by scanning electron microscopy (SEM) (Tandon & Maitra 1983; Srisawangwonk et al. 1989; Ferrer et al. 1996). Oliver et al. (1984) used SEM to study the surfaces of five Trematoda species from frogs, which included *H. similes* and *H. variegates*. Little additional work has been done to study the tegumental surfaces of *Haematoloechus* spp. The present study was undertaken to examine *Haematoloechus* spp. in frogs from the Ohio River Valley region of Indiana and Kentucky. Host specificity, geographical distribution, parasite prevalence and parasite intensities were among the parameters studied. Additionally, SEM was used to examine surface features, with special emphasis on the distribution and morphology of spines, of a representative *H. complexus* specimen.

METHODS

Frogs and toads were collected from five Kentucky counties (Jefferson, Meade, Henry, Oldham and Marion) and two counties in Indiana (Clark and Harrison). Frogs were collected at night by hand or with a frog gig, and immediately placed on ice. The frogs were taken to the laboratory, pithed and examined for parasites within 24 h after collection. They were catalogued by body weight, sex and locality. The lungs were removed and placed in individual containers of physiological saline. Each lung was teased apart under a binocular dissecting microscope.

All lung flukes were washed thoroughly in phosphate buffered saline (PBS) before fixing. Flukes were put in distilled water to allow discharge of eggs and fixed in hot acetic formyl alcohol. The flukes were stained in alcoholic carmine and dehydrated by passage through a graded series of ethyl alcohol. They were then cleared in Terpineol (J.T. Baker, Inc., Phillipsburg, New Jersey) and mounted in Euparal (ASCO Laboratories, Manchester, England).

A representative *H. complexus* specimen was chosen for analysis by SEM. This fluke was washed 3× in PBS and fixed in a cold 3% glutaraldehyde solution buffered to pH 7.3 with cacodylate. As much debris as possible was removed from the surface of the worm by using a camel's hair brush prior to fixing in glutaraldehyde. The specimen was rinsed in PBS, dehydrated through a graded series of acetone, and dried by a brief treatment with hexamethyldisilazane (Sigma Chemical Co., St. Louis, Missouri). It was coated with 50–60 nm of gold in a Polaron PS2 sputter coater, and examined with an ISI-40 scanning electron microscope.

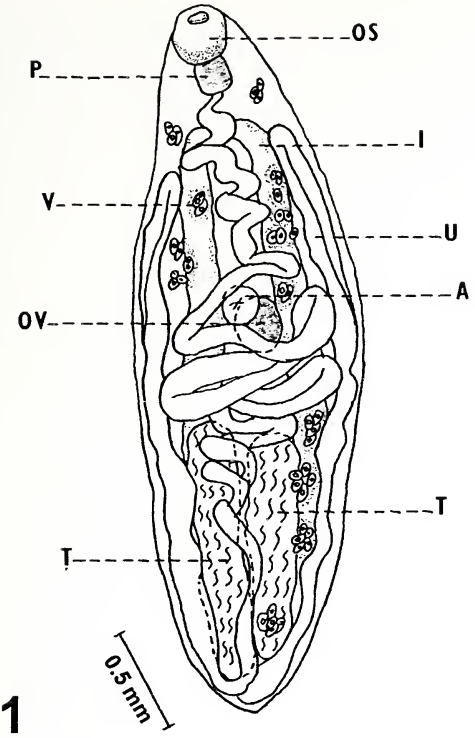
Statistical analysis was performed with the aid of Minitab Statistical Software (Minitab, Inc., State College, Pennsylvania). The relationships between parasites and right and left lung and male and female hosts were examined by comparison of the binomial proportion to the z distribution (Ott 1988). Relationships between host size and lung fluke intensities were analyzed by simple linear regression. A value of $P < 0.01$ was accepted as statistically significant.

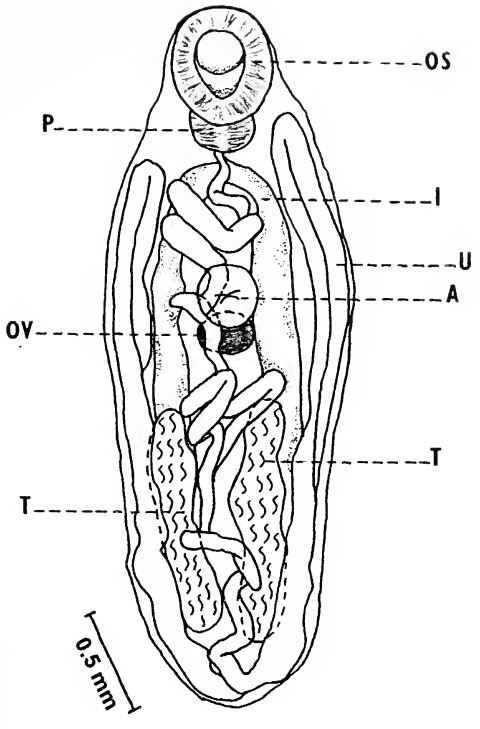
Line drawings of flukes were made by the author with the aid of a Bausch and Lomb microprojector.

RESULTS

Host and parasite species.—One hundred seventy-six frogs and toads were examined for the presence of lung flukes. Of these, 95 were *Rana clamitans* (green frog), 63 were *Rana catesbeiana* (bullfrog), 13 were *Rana utricularia* (southern leopard frog), 3 were *Bufo americanus* (American toad), and one each was *Bufo woodhousii* (Fowler's Toad) and *Hyla chrysocelis* (southern gray treefrog). Of the *R. clamitans* examined, 40 (42%) were infected. Twenty-four (38%) of *R. catesbeiana* were infected. Seven (54%) of the *R. utricularia* were infected. No lung flukes were found in any of the *Bufo* species or the *Hyla chrysocelis* specimen, but samples were very small in these. Of the six recognized species of *Haematoloechus* in North America, four were recovered from the frogs examined in this study. These species included *H. longiplexus*, *H. breviplexus*, *H. varioplexus*, and *H. complexus* (Figs. 1–5). *Haematoloechus longiplexus* specimens from one female *R. catesbeiana* collected from Oldham County, Kentucky had significantly larger oral sucker and acetabulum sizes as compared to other *H. longiplexus* collected during this study (Fig. 2).

Analysis of parasite population parameters.—Of the 23 *H. breviplexus*, all (100%) occurred in *R. catesbeiana*. Of the 63 *H. longiplexus*, 61 (97%) occurred in *R. catesbeiana* and only 2 (3%) were found in *R. clamitans*.





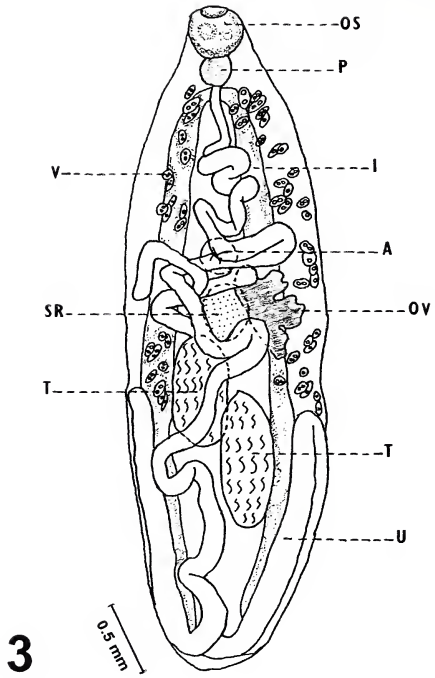
Figures 1, 2.—Line drawings of *Haematoloechus longiplexus* showing variation in sucker sizes. 1. *H. longiplexus*, ventral view; 2. *H. longiplexus*, large sucker size variant, ventral view. *Abbreviations:* A = acetabulum; I = intestine; OS = oral sucker; OV = ovary; P = pharynx; T = testis; U = uterus; V = vitellaria.

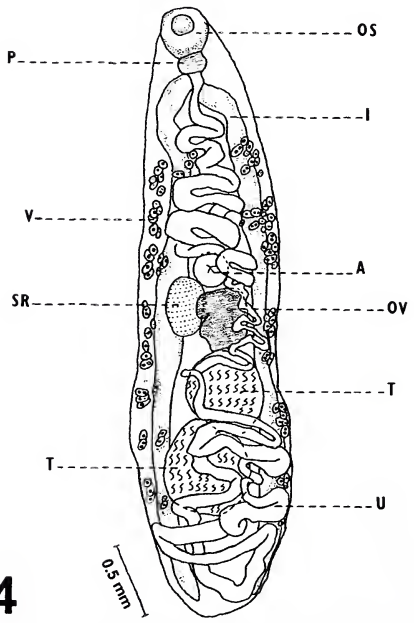
All 8 (100%) *H. varioplexus* were found in a single *R. clamitans* specimen. Of the 412 *H. complexus* found, 316 (77%) occurred in *R. clamitans*, 95 (23%) occurred in *R. utricularia*, and one was found in *R. catesbeiana*. Table 1 compares the prevalence and mean intensities of flukes in their frog hosts. The highest intensity found was 71 mature *H. complexus* found in one *R. clamitans* specimen. Thirty-six were from the right lung and 45 from the left lung. Prevalence of infected frog species was 42% for *R. clamitans*, 38% for *R. catesbeiana* and 54% for *R. utricularia* (Table 1).

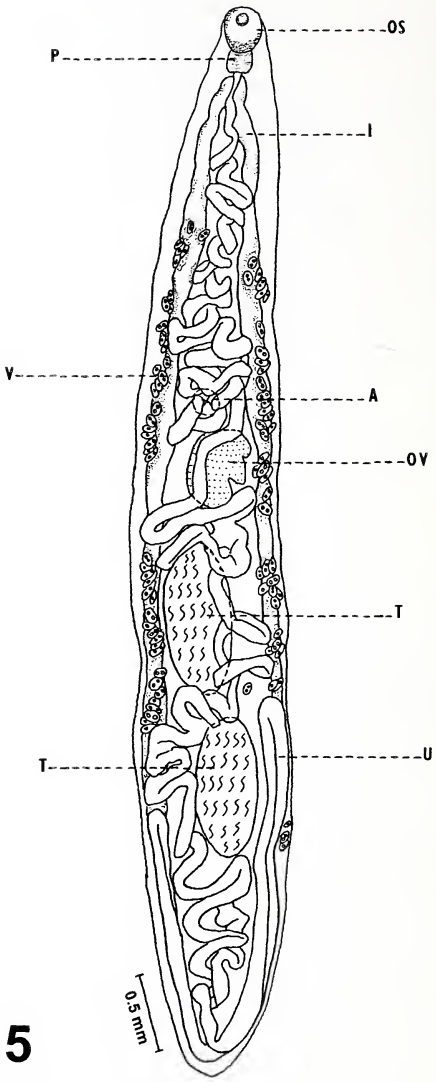
In *R. catesbeiana* the proportion of *H. longiplexus* was higher in the right lung as compared to the left lung. However, the proportion of *H. breviplexus* in the same frog species was higher in the left lung. The overall prevalence of lung flukes between the right and left lung of frog species showed no significant differences. There was also no significant difference in overall intensity of lung flukes with regard to right or left lung. The overall prevalence of lung flukes was significantly higher in male frogs as compared to female frogs ($P < 0.01$). Also there was a significantly higher intensity of lung flukes in male frogs as compared to female frogs ($P < 0.001$). There was no correlation between lung fluke intensity and size (weight) of any of the infected frog species.

Only three frogs had multiple infections of lung fluke species. One *R. catesbeiana* from Marion County, Kentucky was infected with 12 *H. longiplexus* and two *H. complexus*. Another *R. catesbeiana* also from Marion County, Kentucky was infected with seven *H. longiplexus* and four *H. breviplexus*. A *R. clamitans* specimen from Henry County, Kentucky was infected with one each of *H. complexus* and *H. longiplexus*. All *R. utricularia* were infected with only *H. complexus*. Fifteen frogs (21% of infected frogs) harbored immature lung flukes. Flukes were considered to be immature by either absence of eggs in the uterus or incomplete egg development.

To analyze the possibility of a crowding ef-







Figures 3–5.—Line drawings of three species of Haematoloechus. 3. *H. breviplexus*, ventral view; 4. *H. complexus*, ventral view; 5. *H. varioplexus*, ventral view. *Abbreviations:* A = acetabulum; I = intestine; OS = oral sucker; OV = ovary; P = pharynx; SR = seminal receptacle; T = testis; U = uterus; V = vitellaria.

Table 1.—Prevalence and intensities of *Haematoloechus* spp. in infected frogs. * Percentage of infected frogs. † No. of lung flukes per infected frog. NA, Not Appliable.

Frog species	Fluke species	No. examined	No. infected	Prevalence*	Mean intensity†	Highest intensity
Rana clamitans	*H. longiplexus*	95	40	42	8.9	71
	H. complexus					
Rana catesbeiana	*H. breviplexus*	63	24	38	6.3	56
	H. longiplexus					
	H. complexus					
Rana utricularia	*H. complexus*	13	7	54	13.6	33
Bufo americanus	—	3	0	—	—	—
Bufo woodhousii	—	1	0	—	—	—
Hyla chrysocelis	—	1	0	—	—	—
Total	—	176	71	40	NA	NA

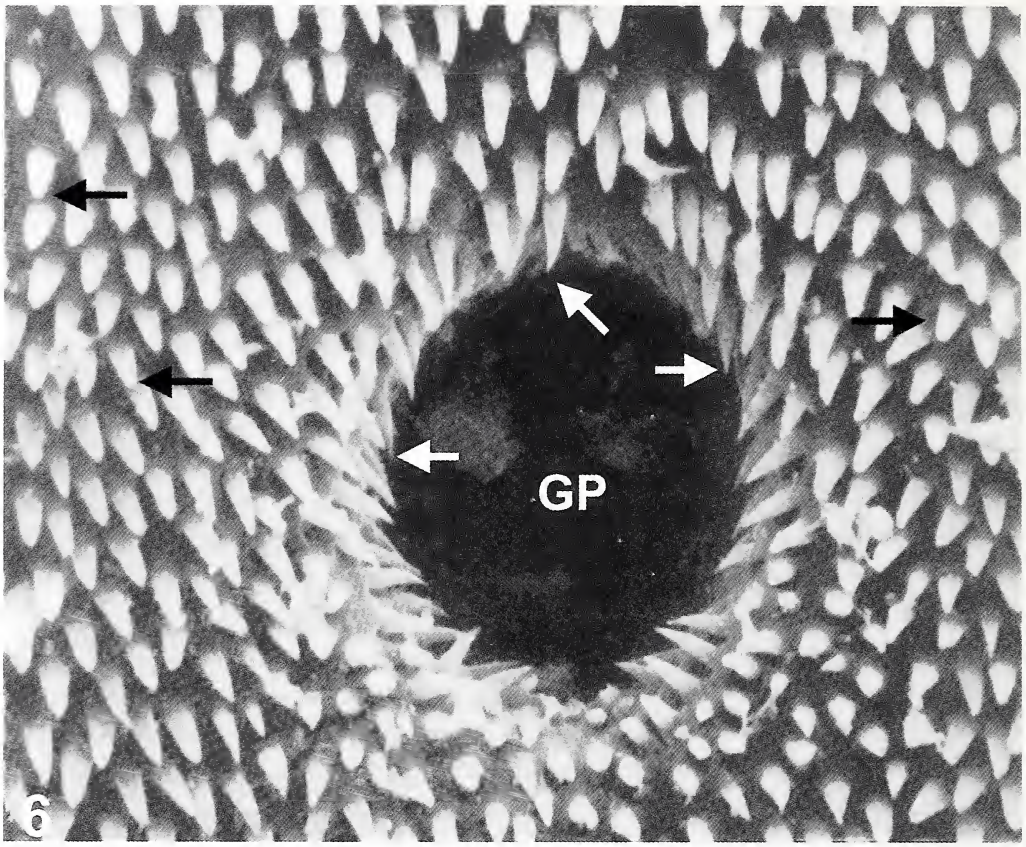
fect of the 71 *H. complexus* found in one frog, each of the measured characters was compared to the same character from the rest of the *H. complexus*. There was no decrease in these characters, as would be expected if there were a crowding effect; instead, all of the characters except for the ratio between the diameter of the oral sucker and that of the acetabulum (O/A ratio) and the ratio between the diameter of the oral sucker and that of the pharynx (O/P ratio) showed a significant increase in size as compared to the rest of the *H. complexus* population ($P < 0.01$).

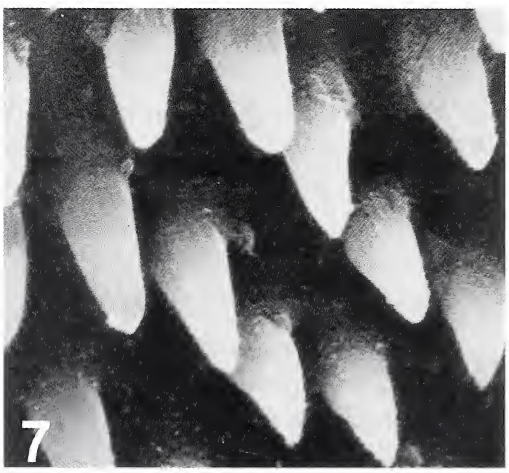
Analysis of the *H. longiplexus* specimens with the larger than average sucker sizes revealed the following results. The oral sucker, pharynx and acetabulum sizes were all significantly larger than in the rest of the *H. longiplexus* found ($P < 0.001$). Although these structures were considerably larger than average, there was no significant difference in O/A ratio, O/P ratio or length and width of these flukes as compared to the rest of the *H. longiplexus* population.

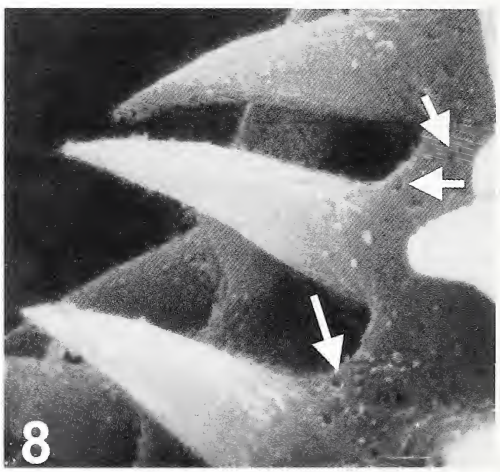
Scanning electron microscopy.—The tegumental surface of a representative specimen of *H. complexus* was studied by SEM. Special emphasis was on the distribution and morphology of the spines. The elongate body of the fluke was covered with spines, except for the rim of the oral sucker. Two distinct spine types could be seen. These included flattened conical-shaped spines (Figs. 6, 7) covering the entire body (except the aspinose rim of the oral sucker) and sharply-attenuated spines seen primarily around the periphery of the genital pore (Figs. 6, 8). The sharply-attenuated spines could also been seen around the periphery of the rim of the oral sucker (Fig. 9). All spines were directed posteriorly except for those surrounding the genital pore (Fig. 6). The inner rim of the oral sucker is aspinose and has a spongy pitted appearance (Fig. 10). The tegument between spines can also be seen to have numerous pores or pits (Fig. 8). No sensory papillae could be identified.

DISCUSSION

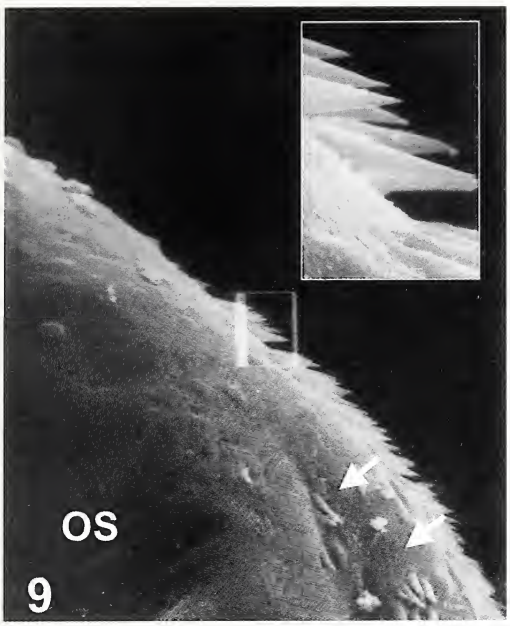
Haematoloechus is one of the most common genera of trematodes found in frogs. The sample of frogs studied consisted of six species with 40% infected with *Haematoloechus* spp. A total of four *Haematoloechus* spp. was recovered from this sample, two of which (*H.*

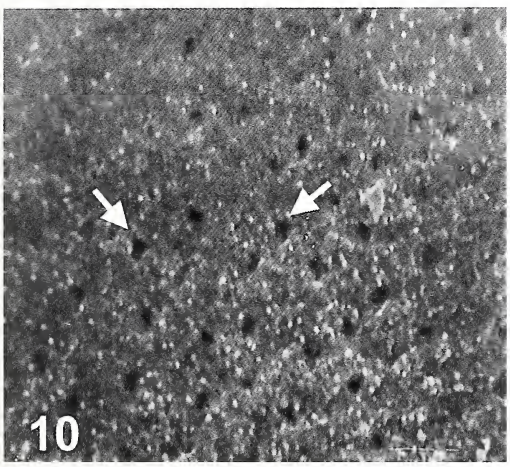






Figures 6–8.—Scanning electron micrographs of the spines of *Haematoloechus complexus*. 6. SEM of genital pore (GP) showing sharply-attenuated spines (white arrows) around the periphery and conical shaped body spines (black arrows) (1000×); 7. Conical shaped body spines (5000×); 8. Sharply-attenuated spines seen around the periphery of the genital pore. Numerous pores are seen in the tegument at the base of the spines (arrows) (10,000×).





Figures 9, 10. Oral sucker of *Haematoloechus*. 9. SEM of the rim of the oral sucker (OS) showing the aspinose, porous inner margin and the sparsely spine-covered outer margin (arrows) (930×). Some sharply-attenuated spines can be seen around the periphery of the oral sucker (inset) (9300×); 10. Spongy surface of the oral sucker with numerous pores (arrows) (10,000×).

complexus and *H. varioplexus*) has not been reported from either Kentucky or Indiana and therefore constitutes a new geographical distribution for these two species.

Of the six species of frogs collected, only the three *Rana* spp. were infected. Neither of the *Bufo* spp. nor the *Hyla chrysocelis* was infected. Even though the numbers of *Bufo* and *Hyla* specimens examined were few, this lack of infection is consistent with other amphibian parasite surveys. These two genera are more terrestrial in their habitats and usually return to the water only to mate. This gives them only limited exposure to infected intermediate hosts of *Haematoloechus* spp. On the other hand, *Rana* spp. live in aquatic environments where there are ample opportunities to eat infected dragonflies or damselflies.

There was no correlation between size of frogs examined and presence of lung flukes in any of the three frog species collected. There was a wide range of sizes among infected frogs for all three *Rana* spp. The largest size range occurred with *R. catesbeiana* in which there were infected frogs from 15.6–203.5 g. Other studies (Dronen 1977) which have examined the relationship between frog weight and lung fluke infections have indicated that *R. catesbeiana* smaller than 20 g were rarely infected with *Haematoloechus* spp. The findings of this study were consistent with those of Dronen (1977) in that only one infected *R. catesbeiana* specimen was less than 20 g.

Although *Haematoloechus* spp. are capable of developing in more than one frog species, they are mainly associated with only one or two species of frogs and rarely other genera, e.g., *Bufo* spp. In the frog sample studied, *R. clamitans* harbored mainly *H. complexus*; *R. utricularia* harbored exclusively *H. complexus*; and *R. catesbeiana* harbored mainly *H. longiplexus* and *H. breviplexus*. One species of lung fluke, *H. varioplexus*, was found exclusively in one *R. clamitans* frog. There were only three cases of multiple infections. *Haematoloechus longiplexus* and *H. complexus* were found in the same *R. clamitans*; also, the same two species were found in a *R. catesbeiana* specimen. *Haematoloechus longiplexus* and *H. breviplexus* were found coinfecting the same *R. catesbeiana* specimen.

The number of mature flukes is usually not large in naturally-infected frogs, with 10 being the average number in this study. There are exceptional cases, however, in which the number far exceeds the average. A leopard frog examined by Cort (1915) had 42 mature lung flukes; and Fortner (1923) found 72 in one leopard frog, but unfortunately did not state whether these were mature or immature. Krull

(1933) reported 74 mature lung flukes recovered from a single frog. In the current study, the largest number (71) of mature lung flukes was taken from a single *R. clamitans* collected from Henry County, Kentucky. There were no noticeable decreases in any of the measured characters of these flukes as might be expected due to the large number of them in a single host (crowding effect).

The level of parasitism was significantly higher in males than in females. Also, male frogs had a higher intensity of lung flukes than did female frogs. These results are consistent with other studies (Lees 1962; Hollis 1972). The difference in parasitism levels of male and female frogs, which is well-marked during the breeding season and less well-marked during the remainder of the year, may be explained by the fact that the female sex hormones depress the level of parasitism (Lees & Bass 1960).

Haematoloechus longiplexus specimens recovered from a particular frog from Oldham County, Kentucky had unusually large suckers (Fig. 2), the largest measuring 0.56 mm long by 0.53 mm wide with an acetabulum 0.33 mm wide. Cort (1915) reported the oral sucker size of one of his largest *H. longiplexus* being 0.36 mm long by 0.42 mm wide with an acetabulum 0.17 mm wide. More recently, Kennedy (1981) examined 203 *H. longiplexus* specimens and found the largest oral sucker size to be 0.49 mm long by 0.49 mm wide, and the largest acetabulum width was 0.24 mm. Therefore, these large sucker variants appear to be unique among the *Haematoloechus* spp. The significance of this variation in sucker sizes is unknown. Unfortunately, only one frog was collected from this particular site; and no other *H. longiplexus* specimens exhibited this variation. A more extensive survey of *H. longiplexus* could determine if these differences in sucker sizes are due to geographic or host-specific differences.

Spines are a common feature on the surface of many flukes. SEM was used to study the surface tegument of a representative specimen of *H. complexus*, and two distinct spine types were identified. Variations of surface spines have been reported by many other investigators (Tandon & Maitra 1983; Smales & Blankespoor 1984; Srisawangwonk et al. 1989). Variations seen in *H. complexus* included flattened conical-shaped spines covering the entire body and sharply-attenuated spines seen around the periphery of the genital pore and the oral sucker. The reasons for this variation are unclear. This may be a true morphological variation, or it may be due to the attenuated spines receiving less direct exposure to the host environment. A pitted tegumental surface has been reported for a number of flukes (Ogbe 1982; Probert & Awad 1987). The entire surface of the fluke, including the rim of the oral sucker, has a porous pitted appearance. The presence of pitting or pores suggests that the tegument may have a secretory function.

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LITERATURE CITED

Andrews, K.D., R.L. Lampley, M.A. Gillman, D.T. Corey, S.R. Ballard, M.J. Blasczyk & W.G. Dyer. 1992. Helminths of *Rana catesbeiana* in Southern Illinois with a checklist of helminths in bullfrogs of North America. Transactions of the Illinois State Academy of Science 85:147–172.

Brooks, D.R. 1976. Parasites of amphibians of the Great Plains. Part 2. Platyhelminths of amphibians in Nebraska. Bulletin of the University of Nebraska State Museum 10:65–92.

Cort, W.W. 1915. North American frog lung flukes. Transactions of the American Microscopical Society 34:203–243.

Dronen, N.O. 1977. Studies on the population structures of two species of *Haematoloechus* Looss, 1899 (Digenea: Plagiorchiidae) in Raniid Frogs in New Mexico. Proceedings of the Helminthological Society of Washington 44:68–72.

Ferrer, J.R, M. Gracenea, M. Trullols & O. Gonzalez-Moreno. 1996. Ultrastructural observations of the tegument of *Postorchigenes gymnesicus* (Digenea: Lecithodendriidae). Journal of Helminthology 70:13–19.

Fortner, H.C. 1923. The distribution of frog parasites of the Douglas Lake Region, Michigan. Transactions of the American Microscopical Society 42:79–90.

Goeze, J.A. 1782. Versuch einer Naturgeschichte der Eingeweidewürmer thierischer Körper. Leipzig.

Goldberg, S.R., C.R. Bursey & H. Cheam. 1998. Helminths of two frog species (*Rana chiricahuensis*, *Rana yavapaiensis*) and one introduced frog species (*Rana catesbeiana*) (Ranidae) from Arizona. Journal of Parasitology 84:175–177.

Harwood, P.D. 1932. The helminths parasitic in the Amphibia and Reptilia in Houston, Texas and vicinity. Proceedings of the United States National Museum 81:1–71.

Hollis, P.D. 1972. Host sex influence on the seasonal incidence of *Haematoloechus medioplexus* (Trematoda: Plagiorchiidae) in *Rana pipiens*. Journal of Parasitology 58:128.

Ingles, L.G. 1932. Four new species of *Haematoloechus* (Trematoda) from *Rana aurora draytoni* from California. University of California Publications in Zoology 37:189–201.

Ingles, L.G. 1936. Worm parasites of California amphibia. Transactions of the American Microscopical Society 55:73–92.

Kennedy, M.J. 1981. A revision of species of the genus *Haematoloechus* Looss, 1899 (Trematoda: Haematoloechidae) from Canada and the United States. Canadian Journal of Zoology 59:1836–1846.

Krull, W.H. 1931. Life history studies on two frog lung flukes, *Pneumonoeces medioplexus* and *Pneumonoeces parviplexus*. Transactions of the American Microscopical Society 50:215–277.

Krull, W.H. 1933. Studies on the life history of a frog lung fluke, *Haematoloechus complexus* (Seely, 1906) Krull, n. comb. Parasitenkunde 6: 192–206.

Kuntz, R.E. & J.T. Self. 1940. The metazoan parasites of some Oklahoma Anura. Proceedings of the Oklahoma Academy of Science 21:33–34.

Lank, D.R., Jr. 1971. Parasites of the bullfrog in Indiana. Proceedings of the Indiana Academy of Science 81:359–364.

Lees, E. & L. Bass. 1960. Sex hormones as a possible factor influencing the level of parasitization in frogs. Nature 186:1207–1208.

Lees, E. 1962. The incidence of helminth parasites in a particular frog population. Parasitology 52: 95–102.

Looss, A. 1894. Die Distomen Unserer Fische Und Frösche. Bibliographia Zoologica, No. 16. 226 pp.

Looss, A. 1899. Weitere Beiträge zur Kenntniss der Trematoden-fauna Aegyptens. Zoologische Jahrbücher Systematik 12:521–784.

Looss, A. 1902. Ueber neue und bekannte Trematoden aus Seeschildkröten. Zoologische Jahrbücher Systematik 16:411–891.

Manter, H.W. 1938. A collection of trematodes from Florida amphibia. Transactions of the American Microscopical Society 57:26–37.

Muzzall, P.M. 1991. Helminth infracommunities of the frogs *Rana catesbeiana* and *Rana clamitans* from Turkey Marsh, Michigan. Journal of Parasitology 77:366–371.

Ogbe, M.G. 1982. Scanning electron microscopy of tegumental surfaces of *Schistosoma margrebowiei* LeRoux, 1933. International Journal of Parasitology 12:191–198.

Oliver, G., R. Bourgat, A. Mouahid & R. Touassem. 1984. The superficial ultrastructure of parasitic Trematoda in amphibians. Zeitschrift für Parasitenkunde 70:499–508.

Ott, L. 1988. An Introduction to Statistical Methods and Data Analysis. 3rd ed. PWS-Kent Publishing Company, Boston, Massachusetts. 231 pp.

Pratt, H.S. 1900. Synopsis of North American invertebrates. XII. The trematodes. Part 2. The Aspidocotyles and the Malacotylea, or digenetic forms. American Naturalist 36:887–910, 953–979.

Probert, A.J. & A.H.H. Awad. 1987. Scanning electron microscopy of the tegument of adult *Schistosoma margrebowiei* LeRoux, 1933, with particular reference to the structure of the tubercles. Parasitology 95:491–498.

Rudolphi, C.A. 1819. Entozoorum Synopsis Cui Accedent Mantissa Duplex Et Indices Locupletissimi. Berlin. 811 pp.

Smales, H.R. & H.D. Blankespoor. 1984. *Echinostoma revolutum* (Froelich, 1802) Looss, 1899 and *Isthmiophora melis* (Schrank, 1788) Luke, 1909 (Echinostomatinae, Digenea). Scanning electron microscopy of the tegumental surfaces. Journal of Helminthology 58:187–195.

Srisawangwonk, T., P. Kanla, S. Tesana & C. Arunganart. 1989. Scanning electron microscopy of the tegumental surface of adult *Haplorchis pumilio* (Looss). Journal of Helminthology 63:141–147.

Stafford, J. 1902a. The American representatives of *Distomum cygnoides*. Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere 17:411–424.

Stafford, J. 1902b. On the American representatives of *Distomum variegatum*. Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere 16:895–912.

Stafford, J. 1905. Trematodes from Canadian vertebrates. Zoologischer Anzeiger 28:681–694.

Stiles, C.W. & A. Hassall. 1894. A preliminary catalogue of the parasites contained in the collection of the United States Bureau of Animal Industry, United States Army Medical Museum, Biological Department of the University of Pennsylvania. Veterinary Magazine 1:245–253.

Tandon, V. & S.C. Maitra. 1983. Surface morphology of *Gastrodiscoides hominis* (Lewis and McConnell, 1876) Leiper, 1913 (Trematoda: Digenea) as revealed by scanning electron microscopy. Journal of Helminthology 57:339–342.

Ulmer, M.J. 1970. Studies on the helminth fauna of Iowa. I. Trematodes of Amphibians. American Midland Naturalist 83:38–64.

Zeder, J.G.H. 1800. Erster Nachtrag Zur Naturgeschichte Der Eingeweidewürmer. Leipzig. 320 pp.

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2002. Proceedings of the Indiana Academy of Science 1:77–94

THE SPIDERS OF ILLINOIS AND INDIANA, THEIR GEOGRAPHICAL AFFINITIES, AND AN ANNOTATED CHECKLIST

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ABSTRACT. The geographical affinities of the 586 spider species currently known from Indiana and Illinois are listed. An annotated checklist of the species is presented.

Keywords: Spiders, Illinois, Indiana, zoogeography

Although many new species have been described in recent years, and more are to be expected, the spider fauna of the United States is still rather incompletely known. The only well-known region of the country is southern New England where 611 species have been recorded by the most recent summary (Kaston 1981).

A few other areas have been sufficiently well-worked that statements about their faunas may be of significance, and here I report on one of these—Illinois and Indiana. The known spider fauna of Illinois stands at present at 550 species, that of Indiana, which has been less intensively studied, at 367. The total for the two states is 586 species (Table 1). Published checklists for these states include, for Illinois, Kaston (1955), Moulder (1966, 1992), and Beatty & Nelson (1979); for Indiana the most recent summary (Parker 1969) cites and summarizes previous publications. Probably over 600 species will eventually be recorded from Illinois and almost as many from Indiana. There are probably very few species of spiders known from either of these states that do not occur also in the other. Among the exceptions are cave-inhabiting species from Indiana, the cave region of which is somewhat isolated from that of Illinois.

Comparison of this checklist with those previously published will show many name changes and deletions. These result from recent taxonomic revisions and discovery of errors and duplications in previous publications. The names used here, in most cases, are those of the most recent revisions. For the convenience of the non-specialist, names used in standard references are often retained, even though recent changes may have been made. Alternate names are shown in parentheses. (These names are not necessarily synonyms.) Families, genera and species are listed in alphabetical order.

Many spiders are known to have a wide distribution in eastern North America, about 75% of the Illinois-Indiana fauna having been recorded from New England (Kaston 1981). More specific distributional data are available only from records published in scattered revisionary and ecological papers. Although Moulder (1992) briefly described distributions of some common species, there has been no attempt to summarize the geographical relationships of the entire fauna.

Distributions of the species have been determined, when possible, from the most recent revision. If no recent revision exists data are taken from Kaston (1972), Richman & Cutler (1978), Roth (1988) or other sources. The geographic relationships of these spiders are discussed below and summarized in Table 2. In calculating percentages of the fauna in each geographic area, introduced species (17 species, 2.9% of the total fauna) and those whose ranges are highly restricted, poorly known or anomalous (35 species, 6.0%) are excluded. The percentages are based on the distributions of the remaining 534 species.

The criteria for placement of a species in a particular geographic region are inevitably somewhat subjective. A species here classified as "Eastern" in distribution, for example, ordinarily occurs from southern New England to southern Georgia or northern Florida, and

Table 1.—Illinois and Indiana spider families with number of species known from each state.

	Ill.	Ind.	Total
Agelenidae	20	13	21
Amaurobiidae	4	3	4
Antrodiaetidae	2	0	2
Anyphaenidae	9	5	9
Araneidae	54	36	57
Atypidae	3	1	3
Clubionidae	15	8	16
Corinnidae	11	7	11
Ctenidae	1	1	1
Ctenizidae	1	1	1?
Dictynidae	15	15	20
Dysderidae	1	1	1
Gnaphosidae	44	23	46
Hahniidae	5	3	5
Linyphiidae	81	53	94
Liocranidae	13	5	14
Loxoscelidae	2	1	2
Lycosidae	52	38	55
Mimetidae	4	3	4
Mysmenidae	2	0	2
Nesticidae	1	1	2
Oecobiidae	1	0	1
Oonopidae	1	0	1
Oxyopidae	3	1	3
Philodromidae	22	16	22
Pholcidae	2	2	2
Pisauridae	10	8	10
Salticidae	67	45	68
Scytodidae	1	1	1
Segestriidae	1	1	1
Tetragnathidae	18	16	20
Theridiidae	55	32	56
Theridiosomatidae	1	1	1
Thomisidae	24	23	26
Uloboridae	3	2	3
Zoridae	1	1	1

west to the 100th meridian (middle Kansas) or beyond. It may or may not range into peninsular Florida or northern New England. Some species might be classified in a different region by another person, but probably there would be few such changes. It is not likely that such differences of opinion would significantly alter the percentages shown in Table 2.

A checklist of Illinois and Indiana species is presented with the geographic area of occurrence of each species indicated. This list is in part a compilation. It has not been possible to examine specimens of every species included in the list. Specimens reported from either state in regional faunal lists or ecological publications, unless the specimens have been examined by the most recent reviser, are not necessarily correctly identified. In families that have not recently been revised in entirety (the Linyphiidae, especially) changes of names and additions or deletions of species are to be expected. Brief notes on some species are presented in the checklist.

Table 2.—Summary of North American distributions of Illinois and Indiana spiders.

Area of occurrence	Number of species	Percent of total fauna
Eastern	197	36.8
Northeastern	98	18.4
Northern	85	15.9
Southeastern	73	13.6
Throughout United States	57	10.6
Western	9	1.7
Central	8	1.5
Southern	7	1.3
Uncertain	35	6.0
Introduced	17	2.9

Thirty-five Illinois species listed here have not appeared on any of the previous checklists, and five have been added to the Indiana checklists. Thirty of these have already been recorded in taxonomic revisions (25 species) or faunal lists (5 species). The others have been collected in southern Illinois during the last several years.

GEOGRAPHY

The largest component of the fauna (36.8%) consists of spiders that are distributed throughout most or all of the eastern United States (and often range into Canada or Mexico). Many of these species reach their western limit at or about the 100th meridian of longitude (Fig. 1), but their distributional limits often do not coincide closely with each other. Some of the eastern species extend across the plains to the base of the Rocky Mountains; others are not known from the northeastern or southeastern extremities of the region. Some have outliers in the west, often in the mountains of Utah or neighboring states (Fig. 2), or in Pacific Coast states (Fig. 3).

The non-coincidence of distributions is probably attributable mostly to differences in species tolerances to various climatic conditions, especially temperature and humidity

Figure 1.—An example of an eastern distribution pattern. This is *Theridion glaucescens* Becker (Theridiidae).

Figure 3.—An example of an eastern distribution, with additional populations in Pacific states. The species shown is *Argiope aurantia* Lucas (Araneidae).

(desiccation rate may be more important than humidity itself). The disjunct ranges of some species may have several causes: survival in refugia, recent introductions, failure to recognize separate populations as different species, lack of collecting in intervening areas or, rarely, incorrect locality labels. The presence of disjunct populations of eastern species in western mountains is frequent (Fig. 2), and consistent with the hypothesis that they originally had a wider distribution, which became restricted as a result of climatic changes. Other hypotheses, such as introduction and dispersal, seem less probable.

The second largest group of species (18.4%) has a northeastern distribution, the southern limit of which varies but often lies about at the latitude of North Carolina, somewhat further south than the southern tip of Illinois (Fig. 4). Northern species, reaching their southern limit in northern or central Illinois, compose 15.9% of the fauna, southeastern species 13.6%. Southeastern species are often at or near their northwestern range limit in the southern tip of Illinois (Fig. 5). This sort of distribution is well known for a number of other groups of organisms found, in Illinois, chiefly in the small area of Gulf Coastal Plain

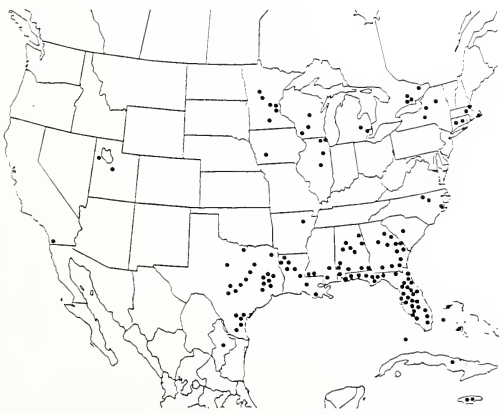

Figure 2.—An example of an eastern distribution pattern, with disjunct populations in western mountains. This is *Mimetus notius* Chamberlin (Mimetidae).

Figure 4.—An example of a northeastern distribution pattern. The species shown is *Sphodros niger* (Hentz) (Atypidae).

Figure 5.—An example of southeastern distribution pattern. The species shown is *Dolichognatha pentagona* (Hentz) (Tetragnathidae).

Figure 6.—An example of a distribution pattern where the species is found throughout the United States. The species shown is *Neoscona arabesca* (Walckenaer) (Araneidae).

that extends into the southern part of the state (DeCosta 1964; Ross 1944; Smith 1961). Ranges of these species may extend in a narrow coastal strip to southern New England under the moderating influence of the Atlantic.

Species found throughout all or most of the United States (Fig. 6) make up 10.6% of the fauna. These may show gaps in their occurrence, not always readily explainable. Some are absent from much of the arid southwest, others from the upper central region, the extreme northeast or extreme southeast. Such distributions are probably largely a result of climatic conditions, perhaps in conjunction with competition by closely-related species. Other influences are probably involved, also, especially lack of collecting in the upper midwest. The remaining three groups contribute little to the total fauna, nine species (1.7%) are predominantly western, eight (1.5%) are central, mostly south central, and seven (1.3%) are southern.

The very small proportion of western and central species suggests that more intensive collecting needs to be done in the little remaining prairie habitat of the states. Perhaps western species were never a significant part of the area's fauna, or they may have been extirpated by destruction of prairie habitats; but some may simply not have been collected.

Seventeen largely synanthropic species are regarded as introduced, primarily from Europe. The only Illinois-Indiana species of the families Dysderidae, Oecobiidae, Pholcidae and Scytodidae are among these. Thirty-five species are so poorly known that their ranges are not determinable. Four of these species, *Ummidia tuobita*, *Ceratinopsis xanthippe*, *C. yola* and *Pirata triens*, are known only from Illinois. They will probably prove to have wider distributions, or to be synonyms of other species.

LITERATURE CITED

Beatty, J.A. & J.M. Nelson. 1979. Additions to the checklist of Illinois spiders. Great Lakes Entomology 12:49–56.

Coyle, F.A. 1968. The mygalomorph spider genus *Atypoides*. Psyche 75:157–194.

DeCosta, J.J. 1964. Latitudinal distribution of chydorid Cladocera in the Mississippi Valley, based on their remains in surficial lake sediments. Investigations of Indiana Lakes and Streams 6:65–101.

Griswold, C.B. 1987. A revision of the jumping spider genus *Habronattus* F.O.P.-Cambridge (Araneae; Salticidae), with phenetic and cladistic analyses. University of California Publications, Entomology 107:1–344.

Hoffman, B.L. 1962. A new genus and species in the diplopod family Nearctodesmidae from Illinois. American Midland Naturalist 68:192–198.

Kaston, B.J. 1955. Check list of Illinois spiders. Transactions of the Illinois Academy of Science 17:165–172.

Kaston, B.J. 1972. How to Know the Spiders. 3rd ed. Wm. C. Brown Co. Dubuque, Iowa.

Kaston, B.J. 1981. Spiders of Connecticut. State Geology and Natural History Survey of Connecticut. Bulletin #70 (rev. ed.). Hartford.

Millidge, A.F. 1983. The erigonine spiders of

North America. Part 6. The genus *Walckenaeria* Blackwall. Journal of Arachnology 11:105–200.

Millidge, A.F. 1987. The erigonine spiders of North America. Part 8. The genus *Eperigone* Crosby and Bishop. American Museum Novitates 2885:1–75.

Moulder, B.C. 1966. Spiders of Illinois: Additional species. Transactions of the Illinois Academy of Science 59:294–295.

Moulder, B.C. 1992. A Guide to the Common Spiders of Illinois. Illinois State Museum Popular Science Series. Vol. X. Springfield.

Ovtsharenko, V.I., G. Levy & N.I. Platnick. 1994. A review of the ground spider genus *Synaphosus*. American Museum Novitates 3095:1–27.

Parker, T.A. 1969. An annotated list of the spiders of Indiana. Proceedings of the Indiana Academy of Science 78:266–314.

Platnick, N.I. & M.U. Shadab. 1988. A revision of the American spiders of the genus *Micaria*. American Museum Novitates 2916:1–64.

Richman, D.B. & B. Cutler. 1978. A list of the jumping spiders of the United States and Canada. Peckhamia 1:82–101.

Ross, H.H. 1944. The caddis flies, or Trichoptera, of Illinois. Bulletin of the Illinois Natural History Survey 23:1–326.

Roth, V.D. (ed.) 1988. Linyphiidae of America north of Mexico. American Arachnological Society. (Unpublished)

Shear, W.A. 1969. A synopsis of the cave millipeds of the United States, with an illustrated key to genera. Psyche 76:126–143.

Smith, P.W. 1961. The amphibians and reptiles of Illinois. Bulletin of the Illinois Natural History Survey 28:1–298.

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Appendix 1.—Checklist of Illinois and Indiana spiders with their areas of distribution in North America. The families and species are listed alphabetically.

	Distribution	Illinois	Indiana
Agelenidae (including part of Amaurobiidae, Cybaeidae, Dictynidae & Hahniidae)			
Agelenopsis emertoni Chamberlin & Ivie	Eastern	X	
Agelenopsis kastoni Chamberlin & Ivie	Northeastern	X	
Agelenopsis naevia (Walckenaer)	Eastern	X	X
Agelenopsis pennsylvanica (C.L. Koch)	Northern	X	X
Agelenopsis potteri (Blackwall)	Northern	X	
Agelenopsis utahana (Ch. & Ive.)	Northern	X	X
Calymmaria cavicola (Banks)	Southeastern	X	X
Cicurina arcuata (= *Cicurina robusta*)	Eastern	X	X
Cicurina brevis (Emerton)	Northeastern	X	X
Cicurina cavealis Bishop & Crosby	Uncertain	X	
Cicurina ludoviciana Simon	Central	X	
Cicurina pallida Keyserling	Northeastern	X	X
Cicurina placida Banks	Northeastern	X	
Coras juvenilis (Keyserling) (= *Coelotes juvenilis*)	Northeastern	X	X
Coras lamellosus (Keyserling)	Eastern	X	X
Coras medicinalis (Hentz)	Eastern	X	'X
Coras taugynus Chamberlin	Southeastern	X	
Cybaeus giganteus Banks (= *C. silicis*)	Uncertain	X	
Tegenaria domestica (Clerck)	Introduced	X	X
Wadotes calcaratus (Keyserling)	Northeastern	X	X
Wadotes hybridus (Emerton)	Northeastern		X
Amaurobiidae (including Titanoecidae)			
Amaurobius bennetti (Blackwall) (= *Callobius bennetti*)	Northeastern	X	X
Amaurobius ferox (Walckenaer)	Introduced	X	X
Titanoeca americana Emerton	Eastern	X	X
Titanoeca brunnea Emerton	Eastern	X	
Antrodiaetidae			
Antrodiaetus unicolor (Hentz)	Eastern	X	
Atypoides hadros Coyle	Uncertain	X	

This species is known only from localities in southern Illinois and southeastern Missouri (Coyle 1968 and personal comm.) The only other species of the genus occur from central California to Oregon. A similar distribution is recorded (Shear 1969) for the millipede genus *Ergodesmus* which includes one species from Illinois (formerly in the genus *Ectopodesmus*), one in the Pacific Northwest and one in Mexico. This has been described as a relict distribution (Hoffman 1962).

Anyphaenidae			
Anyphaena celer (Hentz)	Eastern	X	X
Anyphaena fraterna (Banks)	Eastern	X	X
Anyphaena maculata (Banks)	Southeastern	X	
Anyphaena pectorosa L. Koch	Eastern	X	X
Aysha (*Hibana*) *cambridgei* Bryant	Central	X	
Aysha (*Hibana*) *gracilis* (Hentz)	Eastern	X	X
Oxysoma cubanum Banks	Eastern	X	
Wulfila albens (Hentz)	Southeastern	X	
Wulfila saltabundus (Hentz)	Eastern	X	X
Araneidae			
Acacesia hamata (Hentz)	Southeastern	X	X
Acanthepeira cherokee Levi	Southeastern	X	
Acanthepeira marion Levi	Southeastern	X	
Acanthepeira stellata (Marx)	Eastern	X	X
Araneus bicentenarius (McCook)	Eastern	X	X
Araneus bonsallae (McCook)	Eastern	X	

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Araneus cingulatus (Walckenaer)	Southeastern	X	
Araneus corticarius (Emerton)	Northern		X
Araneus gemmoides Chamberlin & Ivie	Western	X	
Araneus guttulatus (Walckenaer)	Eastern	X	
Araneus juniperi (Emerton) (*Conepeira juniperi*)	Eastern	X	
Araneus marmoreus Clerck	Throughout	X	X
Araneus niveus (Hentz)	Southeastern	X	
Araneus partitus (Walckenaer) (*Conepeira miniata*)	Southeastern	X	
Araneus pegnia (Walckenaer) (*Neosconella pegnia*)	Eastern	X	X
Araneus pratensis (Emerton) (*Singa pratensis*)	Eastern	X	X
Araneus saevus (L. Koch) (*A. solitarius*)	Northern	X	
Araneus thaddeus (Hentz) (*Neosconella thaddeus*)	Eastern	X	X
Araneus trifolium (Hentz)	Northern	X	X
Araniella displicata (Hentz)	Throughout	X	X
Argiope aurantia Lucas	Eastern	X	X
Argiope trifasciata (Forskal)	Throughout	X	X
Cercidia prominens (Westring)	Introduced	X	
Cyclosa conica (Pallas)	Throughout	X	
Cyclosa turbinata (Walckenaer)	Throughout	X	X
Eustala anastera (Walckenaer)	Throughout	X	X
Eustala cepina (Walckenaer)	Eastern	X	X
Eustala emertoni (Banks)	Southeastern	X	
Gea heptagon (Hentz) (*Gea ergaster*)	Southeastern	X	
Hypsosinga funebris (Keyserling)	Throughout	X	
Hypsosinga pygmaea (Sundevall) (*Singa variabilis*)	Northern	X	X
Hypsosinga rubens (Hentz) (*Singa nigripes*)	Eastern	X	X
Larinia borealis Banks	Throughout	X	
Mangora gibberosa (Hentz)	Eastern	X	X
Mangora maculata (Keyserling) (*Mangora ornata*)	Eastern	X	X
Mangora placida (Hentz)	Eastern	X	X
Mastophora bisaccata (Emerton)	Eastern	X	X
Mastophora cornigera (Hentz)	Southern		X
Mastophora hutchinsoni Gertsch	Northeastern	X	
Mastophora phrynosoma Gertsch	Northeastern	X	
Metazygia calix (Walckenaer) (*Alpaida calix*)	Southeastern	X	
Metepeira labyrinthea (Hentz)	Eastern	X	X
Micrathena gracilis (Walckenaer)	Eastern	X	X
Micrathena mitrata (Hentz)	Eastern	X	X
Micrathena sagittata (Walckenaer)	Eastern	X	X
Neoscona arabesca (Walckenaer)	Throughout	X	X
Neoscona crucifera (Lucas) (*N. sacra, N. hentzii*)	Eastern	X	X
Neoscona domiciliorum (Hentz)	Eastern	X	X
Neoscona oaxacensis (Keyserling)	Western		X
Neoscona pratensis (Hentz)	Eastern	X	X
Nuctenea (*Larinioides*) *cornuta* (Clerck) (*Araneus cornutus*)	Throughout	X	X
Nuctenea (*Larinioides*) *patagiata* (Clerck) (*Araneus patagiatus*)	Northern	X	X
Nuctenea (*Larinioides*) *sclopetaria* (Clerck) (*Araneus sericatus, Nuctenea sericata*)	Northern	X	X
Ocrepeira ectypa (Walckenaer) (*Wixia anaglyphe*)	Eastern	X	X
Singa eugeni Levi	Northeastern	X	
Singa keyserlingi McCook	Northeastern	X	
Verrucosa arenata (Walckenaer)	Eastern	X	X
Atypidae			
Sphodros atlanticus Gertsch & Platnick	Uncertain	X	
Sphodros niger (Hentz) (*Atypus milberti*)	Northeastern	X	X

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Sphodros rufipes (Latreille)	Southeastern	X	
Clubionidae s. str.			
Cheiracanthium inclusum (Hentz)	Throughout	X	X
Cheiracanthium mildei L. Koch	Introduced	X	
Clubiona abbotii L. Koch	Eastern	X	X
Clubiona bryantae Gersch	Northern	X	
Clubiona catawba Gertsch	Southeastern	X	
Clubiona johnsoni Gertsch	Northeastern	X	
Clubiona kastoni Gertsch	Northern	X	
Clubiona maritima L. Koch (*C. tibialis*)	Eastern	X	X
Clubiona moesta Banks	Northern	X	
Clubiona obesa Hentz	Northeastern	X	X
Clubiona pygmaea Banks	Eastern	X	X
Clubiona rileyi Gertsch	Northeastern		X
Clubiona riparia L. Koch	Northern	X	X
Clubiona saltitans Emerton	Eastern	X	
Clubionoides (*Elaver*) *excepta* (L. Koch) (*Clubiona pallens*)	Eastern	X	X
Strotarchus piscatorius (Hentz)	Southeastern	X	
Corinnidae (Clubionidae s. lat.)			
Castianeira alata Muma	Uncertain	X	
Castianeira amoena (C.L. Koch)	Southeastern	X	
Castianeira cingulata (C.L. Koch)	Eastern	X	X
Castianeira crocata (Hentz)	Southeastern	X	X
Castianeira descripta (Hentz)	Eastern	X	X
Castianeira gertschi Kaston	Eastern	X	
Castianeira longipalpa (Hentz)	Throughout	X	X
Castianeira trilineata (Hentz)	Eastern	X	X
Castianeira variata Gertsch	Eastern	X	
Meriola decepta Banks (*Trachelas deceptus*)	Southern	X	X
Trachelas tranquillus (Hentz) (*T. ruber*)	Eastern	X	X
Ctenidae			
Anahita punctulata (Hentz) (*A. animosa*)	Southeastern	X	X
Ctenizidae			
Ummidia tuobita (Chamberlin)	Uncertain	X	X?
Kaston gives the type locality as Salem, Illinois. The only mention of Salem in the original description of the species refers to the Peabody Academy of Science in Salem, Massachusetts.			
Dictynidae			
Argenna obesa Emerton	Northern	X	
Dictyna angulata Emerton	Northeastern		X
Dictyna annulipes (Blackwall)	Northern	X	X
Dictyna bellans Chamberlin (*D. longispina*)	Central	X	
Dictyna bicornis Emerton	Eastern	X	X
Dictyna bostoniensis Emerton	Northern	X	X
Dictyna coloradensis Chamberlin	Throughout	X	X
Dictyna cruciata Emerton	Eastern	X	X
Dictyna foliacea (Hentz)	Eastern	X	X
Dictyna formidolosa Gertsch & Ivie	Eastern	X	X
Dictyna hentzi Kaston	Northeastern	X	
Dictyna manitoba Ivie	Western	X	
Dictyna maxima Banks	Northeastern		X
Dictyna minuta Emerton	Northern	X	X
Dictyna sublata (Hentz)	Eastern	X	X
Dictyna volucripes Keyserling	Eastern	X	X

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Lathys foxii (Marx)	Northeastern		X
Lathys immaculata (Chamberlin & Ivie)	Eastern	X	
Lathys maculina Gertsch	Northeastern		X
Lathys pallida (Marx)	Southeastern		X
Dysderidae			
Dysdera crocata C.L. Koch	Introduced	X	X
Gnaphosidae			
Callilepis imbecilla (Keyserling)	Southeastern	X	X
Callilepis pluto Banks	Northern	X	
Cesonia bilineata (Hentz)	Eastern	X	X
Drassodes neglectus (Keyserling)	Northern	X	X
Drassodes saccatus (Emerton) (*D. robinsoni*)	Throughout	X	
Drassyllus aprilinus (Banks)	Eastern	X	X
Drassyllus covensis Exune	Southeastern	X	
Drassyllus creolus Chamberlin & Gertsch	Eastern	X	X
Drassyllus depressus (Emerton)	Northern	X	X
Drassyllus dixinus Chamberlin	Southeastern	X	
Drassyllus eremitus Chamberlin (*D. emeritus*)	Eastern	X	
Drassyllus fallens Chamberlin	Northeastern	X	
Drassyllus frigidus (Banks)	Eastern	X	
Drassyllus lepidus (Banks)	Southern	X	
Drassyllus niger (Banks)	Northern	X	
Drassyllus novus (Banks) (*D. virginianus*)	Eastern	X	X
Drassyllus rufulus (Banks)	Eastern	X	X
Gnaphosa fontinalis Keyserling	Eastern	X	
Gnaphosa sericata (L. Koch)	Eastern	X	X
Haplodrassus bicornis (Emerton)	Northern	X	X
Haplodrassus mimus Chamberlin	Eastern	X	
Haplodrassus signifer (C.L. Koch)	Throughout	X	X
Herpyllus ecclesiasticus Hentz (*H. vasifer*)	Eastern	X	X
Litopyllus temporarius Chamberlin (*L. rupicolens*)	Eastern	X	X
Micaria delicatula Bryant? (*M. aurata*)	Uncertain	X	

Reported only from eastern seaboard states by Platnick & Shadab (1988). The identity of the species recorded from Illinois as *M. aurata* has been confused in the past. Specimens called by this name are now assigned to two different species. Illinois specimens must be re-examined to determine their identity.

Micaria elizabethae Gertsch	Northeastern		X
Micaria laticeps Emerton	Northern	X	
Micaria longipes Emerton	Throughout	X	
Micaria pulicaria (Sundevall)	Throughout	X	
Nodocion floridanus (Banks)	Eastern		X
Sergiolus capulatus (Walckenaer) (*S. variegatus*)	Eastern	X	X
Sergiolus decoratus Kaston	Southeastern	X	
Sergiolus minutus (Banks)	Southeastern	X	
Sergiolus montanus (Emerton)	Throughout	X	X
Sergiolus ocellatus (Walckenaer)	Eastern	X	
Sergiolus tennesseensis Chamberlin	Northeastern	X	X
Sosticus insularis (Banks)	Eastern	X	X
Sosticus loricatus (L. Koch) (*Sostogeus zygethus*)	Northern	X	
Synaphosus paludis (Chamberlin & Gertsch)	Southeastern	X	

Ovtsharenko et al. (1994) state that this species does not belong to the genus *Synaphosus*, but that it can not yet be placed in any other genus. They also suggest it is introduced, possibly from Africa.

Talanites exlineae (Platnick & Shadab) (*Rachodrassus exlineae*)	Southeastern	X	
Trachyzelotes lyonneti (Audouin)	Introduced	X	

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Urozelotes rusticus (L. Koch) (*Drassylus rusticus, Haplodrassus magister*)	Introduced	X	
Zelotes duplex Chamberlin	Eastern	X	X
Zelotes fratris Chamberlin (*Z. subterraneus*)	Northern	X	X
Zelotes hentzi Barrows	Throughout	X	X
Zelotes laccus (Barrows)	Eastern	X	X
Hahniidae			
Antistea brunnea (Emerton)	Northern	X	
Hahnia cinerea Emerton	Throughout	X	X
Hahnia flaviceps Emerton	Southeastern	X	
Neoantistea agilis (Keyserling)	Throughout	X	X
Neoantistea magna (Keyserling) (*N. riparia*)	Northern	X	X
Linyphiidae			
Bathyphantes alboventris (Banks)	Northeastern	X	
Bathyphantes (*Diplostyla*) *concolor* (Wider)	Northern	X	X
Bathyphantes pallidus (Banks)	Northern	X	X
Bathyphantes weyeri (Emerton)	Northeastern		X
Centromerus cornupalpis (O.P.-Cambridge)	Northeastern	X	X
Centromerus latidens (Emerton)	Northeastern	X	X
Ceraticelus atriceps (O.P.-Cambridge)	Northern	X	
Ceraticelus bulbosus (Emerton)	Northern	X	
Ceraticelus creolus Chamberlin	Southeastern	X	
Ceraticelus emertoni (O.P.-Cambridge)	Northeastern	X	X
Ceraticelus fissiceps (O.P.-Cambridge)	Northern	X	X
Ceraticelus laetabilis (O.P.-Cambridge)	Northeastern	X	
Ceraticelus laetus (O.P.-Cambridge)	Northeastern		X
Ceraticelus limnologicus Crosby & Bishop	Eastern	X	X
Ceraticelus micropalpis (Emerton)	Northeastern	X	
Ceraticelus minutus (Emerton)	Northeastern	X	X
Ceraticelus similis (Banks)	Northeastern	X	
Ceratinella brunnea Emerton	Northeastern	X	X
Ceratinops rugosus (Emerton)	Northeastern	X	X
Ceratinopsidis formosa (Banks)	Northeastern	X	
Ceratinopsis (*Tutaibo*) *anglicana* (Hentz)	Southeastern	X	X
Ceratinopsis interpres (O.P.-Cambridge)	Eastern		X
Ceratinopsis laticeps Emerton	Northeastern	X	
Ceratinopsis nigriceps Emerton	Northeastern	X	
Ceratinopsis nigripalpis Emerton (*C. tarsalis*)	Northeastern	X	
Ceratinopsis purpurescens (Keyserling) (*C. styloctetor*)	Eastern	X	
Ceratinopsis sutoris Bishop & Crosby	Southeastern	X	
Ceratinopsis xanthippe (Keyserling)	Uncertain	X	
Ceratinopsis yola Chamberlin & Ivie	Uncertain	X	
Diplocentria bidentata (Emerton) (*Scotoussa bidentata*)	Northern	X	
Eperigone antraea (Crosby)	Uncertain	X	
Recorded only from the Southwest and Mexico by Millidge (1987). Illinois specimens possibly misidentified.			
Eperigone eschatologica Crosby	Southern	X	
Eperigone fradeorum (Berland)	Southeastern	X	
Eperigone maculata (Banks)	Eastern	X	
Eperigone tridentata (Emerton)	Eastern	X	X
Eperigone trilobata (Emerton)	Throughout	X	
Eperigone undulata (Emerton) (*E. contorta*?)	Northern	X	X
Millidge (1987) reports this species only from Canada and the northern tier of states of the U.S. Identity of Illinois and Indiana specimens should be rechecked.			

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Eridantes erigonoides (Emerton)	Northeastern	X	X
Erigone aletris Crosby & Bishop	Northern		X
Erigone atra Blackwall	Northeastern	X	X
Erigone autumnalis Emerton	Eastern	X	X
Erigone blaesa Crosby & Bishop	Northern	X	X
Erigone dentigera O.P.-Cambridge	Eastern	X	X
Erigone infernalis Keyserling	Uncertain	X	X
Floricomus plumalis (Crosby)	Northeastern	X	
Floricomus rostratus (Emerton)	Northeastern	X	
Florinda coccinea (Hentz)	Southeastern	X	X
Frontinella communis (Hentz)	Throughout	X	X
Glyphesis scopulifera (Emerton)	Northeastern	X	
Gonatium crassipalpum Bryant (*Gonatium rubens*)	Northern	X	
Goneatara platyrhinus (Crosby & Bishop)	Eastern		X
Grammonota inornata Emerton	Northeastern	X	X
Grammonota pictilis (O.P.-Cambridge)	Northeastern	X	
Graphomoa theridioides Chamberlin	Southeastern	X	
Halorates (*Collinsia*) *oxypaederotipa* (Crosby)	Northeastern		X
Halorates (*Collinsia*) *plumosa* (Emerton)	Northern	X	X
Hypselistes florens (O.P.-Cambridge)	Northeastern	X	X
Islandiana flaveola (Banks)	Northern	X	
Islandiana longisetosa (Emerton)	Northeastern	X	X
Lepthyphantes (*Megalepthyphantes*) *nebulosa* (Sundevall)	Northeastern	X	X
Lepthyphantes (*Tenuiphantes*) *sabulosus* (Keyserling)	Eastern	X	
Lepthyphantes (*Tenuiphantes*) *zebra* (Emerton)	Northern		X
Linyphia (*Neriene*) *clathrata* Sundevall	Northeastern	X	X
Linyphia (*Microlinyphia*) *mandibulata* Emerton	Northern	X	X
Linyphia (*Neriene*) *radiata* Walckenaer (*L. marginata*)	Eastern	X	X
Linyphia (*Neriene*) *variabilis* Banks (*Linyphia maculata*)	Eastern	X	X
Meioneta evadens (Chamberlin)	Uncertain	X	
Meioneta fabra (Keyserling)	Uncertain	X	X
Meioneta micaria (Emerton)	Eastern	X	X
Meioneta unimaculata (Banks)	Eastern	X	X
Microneta viaria (Blackwall)	Northern	X	
Montilaira probata (O.P.-Cambridge)	Uncertain		X
Mythoplastoides exiguus (Banks)	Northeastern		X
Oedothorax montifer (Emerton)	Northeastern		X
Origanates rostratus (Emerton)	Eastern	X	X
Paracornicularia bicapillata Crosby & Bishop	Central	X	
Pelecopsis bishopi Kaston	Uncertain		X
Phanetta subterranea Emerton	Eastern	X	X
Pityohyphantes costatus (Hentz)	Northern	X	X
Porrhomma cavernicola (Keyserling)	Uncertain	X	X
Satilatlas arenarius (Emerton) (*Minyriolus arenarius*)	Northeastern	X	
Scylaceus pallidus (Emerton) (*S. pallas*)	Northeastern	X	X
Souessoula parva (Banks)	Southeastern	X	
Stemonyphantes blauveltae Gertsch	Northern	X	X
Tapinopa bilineata Banks	Eastern	X	
Tennesseellum formica (Emerton)	Northern	X	X
Tmeticus ornatus (Emerton)	Northeastern	X	
Walckenaeria brevicornis (Emerton) (*Cornicularia brevicornis*)	Northeastern	X	
Walckenaeria communis (Emerton) (*Cornicularia communis*)	Northern	X	

Millidge's revision of *Walckenaeria* (1983) does not include records of this species from Illinois, but its presence in the state is to be expected. Millidge did not have access to specimens from all U.S. collections, so probably did not see those on which the Illinois records were based.

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Walckenaeria directa (O.P.-Cambridge) (*Cornicularia directa*)	Northern	X	
Walckenaeria indirecta (O.P.-Cambridge) (*Cornicularia indirecta*)	Northeastern	X	
Walckenaeria (*Cornicularia*) *minuta* (Emerton)	Northeastern		X
Walckenaeria spiralis (Emerton) (*W. vigilax*)	Northeastern	X	
Walckenaeria subdirecta Millidge	Eastern	X	X
Liocranidae			
Agroeca minuta Banks	Northeastern	X	
Agroeca pratensis Emerton	Northern		X
Phrurotimpus alarius (Hentz)	Eastern	X	X
Phrurotimpus borealis (Emerton)	Northern	X	X
Phrurotimpus emertoni (Gertsch) (*Scotinella emertoni*)	Uncertain	X	
Phrurotimpus illudens Gertsch	Unceratin	X	
Phrurotimpus minutus (Banks)	Northern	X	X
Scotinella delicatula (Gertsch)	Uncertain	X	
Scotinella formica (Banks)	Northeastern	X	
Scotinella fratrella (Gertsch)	Eastern	X	
Scotinella goodnighti (Muma)	Uncertain	X	
Scotinella pugnata (Emerton)	Northern	X	
Scotinella redempta (Gertsch)	Southeastern	X	
Scotinella similis (Banks)	Northeastern	X	X
Loxoscelidae (Sicariidae)			
Loxosceles reclusa Gertsch & Mulaik	Central	X	X
Loxosceles rufescens (DuFour)	Introduced	X	
Lycosidae			
Allocosa funerea (Hentz) (*Arctosa funerea*)	Eastern	X	X
Allocosa noctuabunda (Montgomery)	Southeastern		X
Allocosa sublata (Montgomery)	Northeastern		X
Arctosa emertoni Gertsch	Northern	X	X
Arctosa littoralis (Hentz)	Throughout	X	X
Arctosa rubicunda (Keyserling)	Northern		X
Geolycosa missouriensis (Banks)	Central	X	X
Geolycosa wrightii (Emerton)	Northern	X	X
The application of the generic name *Lycosa* to North American species is questionable. The name is retained here, used in the broad sense, (including species currently listed under *Gladicosa, Hogna* and *Rabidosa*) until revisionary work currently in progress is published.			
Lycosa aspersa Hentz	Eastern	X	X
Lycosa baltimoriana (Keyserling)	Northern	X	X
Lycosa carolinensis Walckenaer	Throughout	X	X
Lycosa frondicola Emerton	Northeastern	X	X
Lycosa georgicola Walckenaer	Southeastern	X	X
Lycosa gulosa Walckenaer	Eastern	X	X
Lycosa helluo Walckenaer	Eastern	X	X
Lycosa hentzi Banks	Southeastern	X	
Lycosa pulchra (Keyserling)	Southeastern	X	
Lycosa punctulata Hentz	Eastern	X	X
Lycosa rabida Walckenaer	Eastern	X	X
Pardosa distincta (Blackwall)	Uncertain	X	
Pardosa fuscula (Thorell)	Northern	X	X
Pardosa lapidicina Emerton	Northeastern	X	X
Pardosa milvina (Hentz)	Northeastern	X	X

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Pardosa modica (Blackwall)	Northern	X	X
Pardosa moesta Banks	Northern	X	X
Pardosa saxatilis (Hentz)	Northeastern	X	
Pardosa xerampelina (Keyserling)	Northern	X	X
Pirata alachua Gertsch & Wallace (*P. alachuus*)	Southeastern	X	X
Pirata apalacheus Gertsch	Southeastern	X	X
Pirata aspirans Chamberlin (*P. arenicola*)	Northeastern	X	
Pirata giganteus Gertsch	Uncertain	X	
Pirata insularis Emerton	Eastern	X	X
Pirata (*Trebacosa*) *marxi* Stone	Northeastern	X	X
Pirata minutus Emerton	Eastern	X	X
Pirata montanoides Banks	Uncertain	X	
Pirata montanus Emerton	Northeastern	X	X
Pirata piraticus (Clerck)	Northern	X	X
Pirata sedentarius Montgomery (*P. maculatus*)	Throughout	X	X
Pirata spiniger (Simon)	Southeastern	X	
Pirata sylvanus Chamberlin & Ivie	Southeastern	X	
Pirata triens Wallace & Exline	Uncertain	X	
Pirata zelotes Wallace & Exline	Northeastern	X	
Schizocosa aulonia Dondale	Central	X	
Schizocosa avida (Walckenaer) (*Lycosa avida*)	Eastern	X	X
Schizocosa bilineata (Emerton)	Eastern	X	X
Schizocosa crassipalpis (Emerton) (*S. crassipalpata*)	Northeastern	X	X
Schizocosa mccooki (Montgomery)	Western	X	
Schizocosa ocreata (Hentz) (*S. crassipes*)	Eastern	X	X
Schizocosa retrorsa (Banks)	Eastern	X	
Schizocosa rovneri (Uetz & Dondale)	Uncertaain	X	
Schizocosa saltatrix (Hentz)	Eastern	X	X
Schizocosa stridulans Stratton	Uncertain	X	
Trochosa (*Varacosa*) *avara* Keyserling (*Lycosa avara*)	Eastern	X	X
Trochosa (*Varacosa*) *shenandoa* (Chamberlin & Ivie)	Eastern	X	
Trochosa terricola Thorell (*T. pratensis*)	Throughout	X	X
Mimetidae			
Ero furcata (Villers)	Throughout	X	X
Mimetus epeiroides Emerton	Eastern	X	X
Mimetus notius Chamberlin	Eastern	X	
Mimetus puritanus Chamberlin	Eastern	X	X
Mysmenidae			
Maymena ambita (Barrows)	Southeastern	X	
Mysmena (*Microdipoena*) *guttata* (Banks)	Eastern	X	
Nesticidae			
Nesticus carteri Emerton	Uncertain		X
Nesticus pallidus Emerton (*Eidmannella pallida*)	Eastern	X	
Oecobiidae			
Oecobius cellariorum (Duges) (*O. texanus*)	Introduced	X	
Oonopidae			
Orchestina saltitans Banks	Eastern	X	
Oxyopidae			
Oxyopes aglossus Chamberlin	Southeastern	X	
Oxyopes salticus Hentz	Eastern	X	X
Oxyopes scalaris Hentz	Throughout	X	

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Philodromidae (Thomisidae s. lat.)			
Ebo latithorax Keyserling	Eastern	X	X
Ebo pepinensis Gertsch	Western	X	X
Philodromus alascensis Keyserling	Northern	X	X
Philodromus bimuricatus Dondale & Redner	Southeastern	X	
Philodromus cespitum (Walckenaer) (*P. aureolus*)	Northern	X	X
Philodromus imbecillus Keyserling	Throughout	X	X
Philodromus infuscatus Keyserling	Throughout	X	
Philodromus keyserlingi Marx	Eastern	X	X
Philodromus marxi Keyserling	Eastern	X	X
Philodromus minutus Banks	Eastern	X	X
Philodromus montanus Bryant	Southeastern	X	
Philodromus oneida Levi	Northern	X	
Philodromus placidus Banks	Throughout	X	X
Philodromus praelustris Keyserling	Northern	X	X
Philodromus pratariae (Scheffer)	Central	X	
Philodromus rufus Walckenaer	Northern	X	X
Philodromus vulgaris (Hentz) (*P. pernix*)	Eastern	X	X
Thanatus formicinus (Clerck)	Northern	X	X
Thanatus rubicellus Mello-Leitão	Northern	X	
Tibellus duttoni (Hentz)	Eastern	X	X
Tibellus maritimus (Menge)	Northern	X	X
Tibellus oblongus (Walckenaer)	Throughout	X	X
Pholcidae			
Pholcus phalangioides (Fuesslin)	Introduced	X	X
Spermophora senoculata (Duges) (*S. meridionalis*)	Introduced	X	X
Pisauridae			
Dolomedes albineus Hentz	Southeastern	X	
Dolomedes scriptus Hentz	Eastern	X	X
Dolomedes striatus Giebel (*D. fulviatronotatus*)	Northeastern	X	X
Dolomedes tenebrosus Hentz	Eastern	X	X
Dolomedes triton (Walckenaer) (*D. scapularis*)	Throughout	X	X
Dolomedes vittatus Walckenaer (*D. urinator*)	Eastern	X	X
Pisaurina brevipes (Emerton)	Eastern	X	X
Pisaurina dubia (Hentz)	Southeastern	X	
Pisaurina mira (Walckenaer)	Eastern	X	X
Pisaurina undulata (Keyserling)	Southeastern	X	X
Salticae			
Admestina tibialis (C.L. Koch)	Eastern	X	X
Agassa cyanea (Hentz) (*A. cerulea*)	Eastern	X	X
Ballus (*Attidops*) *youngii* Peckhams	Northeastern	X	
Eris aurantia (Lucas) (*Paraphidippus aurantius*)	Southeastern	X	X
Eris flava (Peckhams) (*Paraphidippus flavus*)	Eastern	X	
Eris militaris (Hentz) (*Paraphidippus marginatus, E. marginata*)	Throughout	X	X
Eris pinea (Kaston)	Uncertain	X	X
Evarcha hoyi (Peckhams)	Northern	X	X
Ghelna canadensis (Banks) (*Metaphidippus canadensis*)	Northeastern	X	X
Habrocestum parvulum (Banks)	Eastern	X	
Habrocestum pulex (Hentz)	Eastern	X	X
Habronattus agilis (Banks)	Eastern	X	X
Possibly misidentified, recorded by Griswold (1987) only from East Coast.			
Habronattus borealis (Banks)	Northeastern	X	X

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Habronattus calcaratus (Banks)	Southeastern	X	X
Habronattus coecatus (Hentz) (*H. coronatus*)	Eastern	X	
Habronattus cognatus (Peckhams) (*H. arizonensis*)	Central	X	X
Habronattus decorus (Blackwall)	Eastern	X	
Habronattus texanus (Chamberlin) (*H. rutherfordi*)	Uncertain	X	
Habronattus viridipes (Hentz)	Throughout	X	
Hasarius adansonii (Audouin)	Introduced	X	X
Hentzia mitrata (Hentz)	Eastern	X	X
Hentzia palmarum (Hentz)	Eastern	X	X
Maevia inclemens (Walckenaer)	Eastern	X	X
Marpissa formosa (Banks) (*Hyctia bina, Marpissa bina*)	Eastern	X	X
Marpissa grata (Gertsch)	Uncertain	X	
Marpissa lineata (C.L. Koch) (*Onondaga lineata*)	Eastern	X	X
Marpissa pikei (Peckhams) (*Hyctia pikei*)	Eastern	X	X
Metacyrba taeniola (Hentz)	Southern	X	
Metacyrba (*Platycryptus*) *undata* (DeGeer) (*Marpissa undata*)	Eastern	X	X
Neon nellii Peckhams	Eastern	X	
Peckhamia americana (Peckhams)	Eastern	X	X
Peckhamia picata (Hentz)	Eastern	X	
Pelegrina chalceola Maddison	Southern	X	
Pelegrina exigua (Banks)	Eastern	X	
Pelegrina flavipedes (Peckhams) (*Metaphidippus flavipedes*)	Northern	X	X
Pelegrina galathea (Walckenaer) (*Metaphidippus galathea*)	Eastern	X	X
Pelegrina insignis (Banks) (*Metaphidippus insignis*)	Northeastern	X	X
Pelegrina proterva (Walckenaer) (*Metaphidippus protervus*)	Eastern	X	X
Phidippus audax (Hentz)	Eastern	X	X
Phidippus cardinalis (Hentz)	Eastern	X	X
Phidippus clarus Keyserilng (*P. rimator*)	Throughout	X	X
Phidippus insignarius C.L. Koch (*P. fraudulentus*)	Northeastern	X	X
Phidippus mccooki (Peckhams)	Northeastern	X	X
Phidippus mystaceus (Hentz)	Northeastern	X	
Phidippus pius Scheffer	Uncertain	X	
Phidippus princeps (Peckhams)	Northeastern	X	X
Phidippus purpuratus Keyserling	Southeastern		X
Phidippus putnamii (Peckhams)	Southeastern	X	X
Phidippus whitmani Peckhams	Northeastern	X	X
Phlegra fasciata (Hahn)	Eastern	X	X
Salticus scenicus (Clerck)	Throughout	X	X
Sarinda hentzi (Banks) (*Myrmarachne hentzi*)	Eastern	X	
Sassacus papenhoei Peckhams	Western	X	
Sitticus concolor (Banks) (*S. cursor*)	Eastern	X	
Sitticus palustris (Peckhams)	Northern	X	X
Synageles noxiosus (Hentz) (*Gertschia noxiosa*)	Eastern	X	
Synageles occidentalis Cutler	Western	X	
Synemosyna formica Hentz (*S. lunata*)	Eastern	X	X
Talavera minuta (Banks)	Northern	X	X
Thiodina puerpera (Hentz) (*T. irrorata*)	Eastern	X	
Thiodina sylvana (Hentz)	Southeastern	X	X
Tutelina elegans (Hentz)	Eastern	X	X
Tutelina formicaria (Emerton) (*Icius formicarius*)	Northeastern	X	
Tutelina hartii (Emerton) (*Icius hartii*)	Northeastern	X	X
Tutelina similis (Banks)	Northeastern	X	X
Zygoballus nervosus (Peckhams)	Eastern	X	X
Zygoballus rufipes Peckhams (*Z. bettini*)	Eastern	X	X
Zygoballus sexpunctatus (Hentz)	Southeastern	X	

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Scytodidae			
Scytodes thoracica (Latreille)	Introduced	X	X
Segestriidae			
Ariadna bicolor (Hentz)	Eastern	X	X
Tetragnathidae (Araneidae s. lat.)			
Dolichognatha pentagona (Hentz)	Southeastern	X	
Glenognatha foxi (McCook) (*Mimognatha foxi*)	Eastern	X	X
Leucauge venusta (Walckenaer)	Eastern	X	X
Meta ovalis (Gertsch) (*Meta menardi*)	Northeastern	X	X
Pachygnatha autumnalis Marx	Eastern	X	
Pachygnatha brevis Keyserling	Northeastern	X	X
Pachygnatha dorothea McCook	Northern	X	
Pachygnatha furcillata Keyserling	Eastern		X
Pachygnatha tristriata C.L. Koch	Eastern	X	X
Pachygnatha xanthostoma C.L. Koch	Northern	X	X
Tetragnatha caudata Emerton	Eastern	X	X
Tetragnatha elongata Walckenaer	Eastern	X	X
Tetragnatha extensa (Linnaeus)	Northern		X
Tetragnatha guatemalensis O.P.-Cambridge (*T. seneca*)	Eastern	X	X
Tetragnatha laboriosa Hentz	Throughout	X	X
Tetragnatha pallescens F.O.P.-Cambridge	Eastern	X	X
Tetragnatha shosone Levi	Northern	X	
Tetragnatha straminea Emerton	Eastern	X	X
Tetragnatha vermiformis Emerton	Eastern	X	X
Tetragnatha versicolor Walckenaer	Throughout	X	X
Theridiidae			
Achaearanea globosa (Hentz) (*Hentziectypus globosus*)	Eastern	X	
Achaearanea porteri (Banks)	Eastern	X	X
Achaearanea rupicola (Emerton) (*Theridion rupicola*)	Northeastern	X	X
Achaearanea tepidariorum (C.L. Koch) (*Theridion tepidariorum*)	Introduced	X	X
Anelosimus studiosus (Hentz)	Southeastern	X	
Argyrodes cancellatus (Hentz)	Eastern	X	
Argyrodes elevatus Taczanowski	Southeastern	X	
Argyrodes fictilium (Hentz)	Eastern	X	
Argyrodes trigonum (Hentz)	Eastern	X	X
Crustulina altera Gertsch & Archer	Eastern	X	X
Crustulina sticta (O.P.-Cambridge)	Throughout	X	X
Dipoena nigra (Emerton)	Throughout	X	
Dipoena prona (Menge)	Throughout	X	
Enoplognatha joshua Chamberlin & Ivie (*E. rugosa*)	Western	X	
Enoplognatha marmorata (Hentz)	Throughout	X	X
Enoplognatha tecta Keyserling (*E. caricis*)	Northeastern	X	
Euryopis argentea Emerton	Northern	X	X
Euryopis funebris (Hentz) (*E. limbata*)	Eastern	X	X
Euryopis gertschi Levi	Northeastern	X	X
Euryopis quinquemaculata Banks	Southeastern	X	
Latrodectus mactans (Fabricius)	Southeastern	X	X
Some of the records in Kaston (1955) undoubtedly belong with the next species.			
Latrodectus variolus Walckenaer	Northeastern	X	X
Pholcomma hirsutum Emerton	Eastern	X	X
Phoroncidia americana (Emerton)	Eastern	X	X
Robertus eremophilus Chamberlin	Uncertain	X	
Robertus frontatus (Banks) (*Ctenium frontatus*)	Northeastern	X	

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Robertus laticeps (Keyserling) (*Ctenium laticeps*)	Northeastern	X	
Robertus riparius (Keyserling) (*Ctenium riparius*)	Northeastern	X	X
Spintharus flavidus Hentz	Southeastern	X	
Steatoda albomaculata (DeGeer) (*Lithyphantes albomaculata*)	Northern	X	X
Steatoda americana (Emerton) (*Asagena americana*)	Throughout	X	X
Steatoda borealis (Hentz)	Eastern	X	X
Steatoda grossa (C.L. Koch)	Introduced		X
Steatoda triangulosa (Walckenaer) (*Teutana triangulosa*)	Introduced	X	X
Stemmops ornatus (Bryant)	Southeastern	X	
Theridion alabamense Gertsch & Archer	Eastern	X	X
Theridion albidum Banks	Eastern	X	X
Theridion antonii Keyserling	Southeastern	X	
Theridion berkeleyi Emerton (*T. hemerobium*)	Northeastern	X	
Theridion (*Wamba*) *crispulum* Simon	Southeastern	X	
Theridion differens Emerton	Throughout	X	X
Theridion flavonotatum Becker	Southeastern	X	
Theridion frondeum Hentz	Northern	X	X
Theridion glaucescens Becker (*T. spirale*)	Eastern	X	X
Theridion llano Levi	Uncertain	X	
Theridion lyricum Walckenaer	Eastern	X	X
Theridion murarium Emerton	Throughout	X	X
Theridion neshamini Levi	Uncertain	X	
Theridion pennsylvanicum Emerton	Eastern	X	X
Theridion pictipes Keyserling	Southeastern	X	
Theridion pictum (Walckenaer) (*T. zelotypum*)	Northern	X	X
Theridion punctosparsum Emerton	Southeastern	X	X
Theridion rabuni Chamberlin & Ivie	Uncertain	X	
Theridion opulenta (Walckenaer)	Eastern	X	X
Thymoites pallida (Emerton)	Southern	X	
Thymoites unimaculata (Emerton) (*Theridion unimaculatum*)	Eastern	X	X
Theridiosomatidae			
Theridiosoma gemmosum (L. Koch) (*T. radiosa*)	Eastern	X	X
Thomisidae			
Coriarachne versicolor Keyserling (*C. lenta*)	Eastern	X	X
Misumena vatia (Clerck)	Throughout	X	X
Misumenoides formosipes (Walckenaer)	Throughout	X	X
Misumenops asperatus (Hentz)	Throughout	X	X
Misumenops celer (Hentz) (*M. delphinus*)	Throughout	X	
Misumenops oblongus (Keyserling)	Throughout	X	X
Oxyptila (*Ozyptila*) *americana* Banks (= *O. barrowsi*)	Eastern	X	X
Oxyptila conspurcata Thorell	Northern		X
Oxyptila monroensis Keyserling	Eastern	X	X
Synema parvulum (Hentz)	Southeastern	X	X
Tmarus angulatus (Walckenaer)	Throughout	X	X
Tmarus rubromaculatus Keyserling	Southeastern		X
Xysticus auctificus Keyserling (*X. lemniscatus*)	Southeastern	X	X
Xysticus banksi Bryant	Northeastern	X	X
Xysticus bicuspis Keyserling	Throughout	X	X
Xysticus discursans Keyserling	Throughout	X	X
Xysticus elegans Keyserling	Throughout	X	X
Xysticus emertoni Keysering	Northern	X	
Xysticus ferox (Hentz) (*X. transversatus*)	Throughout	X	X
Xysticus fraternus Banks	Eastern	X	X

Appendix 1.—Continued.

	Distribution	Illinois	Indiana
Xysticus funestus Keyserling (*X. tumefactus*)	Eastern	X	X
Xysticus gulosus Keyserling	Northern	X	X
Xysticus luctans (C.L. Koch)	Northeastern	X	X
Xysticus punctatus Keyserling	Northern		X
Xysticus texanus Banks	Southeastern	X	
Xysticus triguttatus Keyserling	Eastern	X	X
Uloboridae			
Hyptiotes cavatus (Hentz)	Eastern	X	X
Octonoba sinensis (Simon) (*Uloborus octonarius*)	Introduced	X	
Uloborus glomosus Walckenaer (*U. americanus*)	Eastern	X	X
Zoridae			
Zora pumila (Hentz)	Eastern	X	X

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ARE BATS IN INDIANA DECLINING?

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ABSTRACT. The number of big brown bats in Indiana was estimated using an estimated number of colonies per county times the average number of bats per colony times the number of counties in the state. Estimates of the number of individuals of other species in the state were assessed using their relative abundance by mist-netting in relation to the big brown bat. Assessment of population levels over time was made by examining four decades of submission of specimens to the Indiana Department of Health rabies lab. Twelve species of bats are known from Indiana, of which one, Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, occurs only sporadically and is considered of accidental occurrence. *Myotis austroriparius* was known to hibernate in certain caves in south central Indiana through the early 1970's, but it is apparently now extirpated. This leaves ten species of bats in the state. Two – the gray myotis, *Myotis grisescens*, and the Indiana myotis, *Myotis sodalis* – are on the federally-endangered list. However, there is only one colony of gray myotis in the state. It is in Clark County and has increased from about 400 bats in 1982 to about 4000 today. The Indiana myotis has increased from about 124,000 in 1980 to about 173,000 today, whereas rangewide, that species has declined from about 589,000 in 1980 to 381,000 today. Four other species appear to have declined in Indiana since 1980: the evening bat, red bat, hoary bat and little brown myotis. The big brown bat, eastern pipistrelle, and silver-haired bat may have increased. The northern myotis apparently has remained relatively stable over this period.

Keywords: Bats, Chiroptera, populations, Indiana

The world's human population is increasing rapidly, and consequently natural and agricultural land is rapidly disappearing (at a rate of about 102,000 acres per year in Indiana and and that rate of disappearance is rapidly increasing). These forces tend to make it increasingly difficult for many native species to survive as their habitat becomes both reduced and degraded. We therefore thought it would be of interest to attempt to determine whether the various species of bats of Indiana are declining.

Twelve species of bats are known from Indiana (Mumford & Whitaker 1982), including five species of *Myotis*: the southeastern myotis (*M. austroriparius*), gray myotis (*M. grisescens*), little brown myotis (*M. lucifugus*), northern myotis (*M. septentrionalis*, previously known as *M. keenii*), and Indiana myotis (*M. sodalis*). Other species are the big brown bat (*Eptesicus fuscus*), eastern pipistrelle (*Pipistrellus subflavus*), evening bat (*Nycticeius humeralis*), silver-haired bat (*Lasionycteris noctivagans*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), red bat (*Lasiurus borealis*), and hoary bat (*Lasiurus cinereus*).

Since *Mammals of Indiana* was published (Mumford & Whitaker 1982), many studies have been carried out on bats in Indiana, both on individual species and at the community level, using a number of approaches. The biggest problem in determining bat population trends is that often there are not adequate older data to compare to more recent data. Also, data sets are based on different collection methods. It is difficult to estimate the abundance of most of the species of bats, but some approaches can be used to indicate relative population size.

We have accumulated considerable information on some of the bats, particularly *Myotis lucifugus*, *Myotis grisescens*, *M. septentrionalis*, *Myotis sodalis*, *Eptesicus fuscus*, *Nycticeius humeralis*, and *Pipistrellus subfla-*

[1]*Deceased*

vus. Also much work has been done on certain bat communities, particularly those of Prairie Creek in Vigo County, along the Wabash and Ohio Rivers in southwestern Indiana, and at Copperhead Cave (Vermillion County) by Whitaker and associates. Brack and associates and also Whitaker and associates have carried out extensive netting over streams in much of Indiana to determine distribution and summer habitat of *Myotis sodalis* and other species. These studies have occurred in 80 of the 92 counties throughout the state. Another excellent source of information is the data from the Indiana State Department of Health rabies laboratory, since numerous bats have been received over a long period of time (1966 to present). The rabies lab data give relatively good information for all species. In addition, Brack and associates have carried out surveys in winter for *Myotis sodalis* and other bats present in known and suspected *M. sodalis* hibernacula (plus some newly-added ones) every other year since 1980 in accordance with U.S. Fish & Wildlife Service guidelines. Also data collected by netting or with harp traps at cave or mine entrances are pertinent for some species, and the numbers of colonies in buildings are pertinent for others.

This paper has two objectives: (1) to determine if bats in Indiana are declining, and (2) to provide baseline estimates of the total numbers of bats, by species, in the state. It is recognized that these tasks are difficult. However, despite the difficulties, we offer estimates of the total number of each species present in the state, and determine whether the various species are stable, increasing, or decreasing.

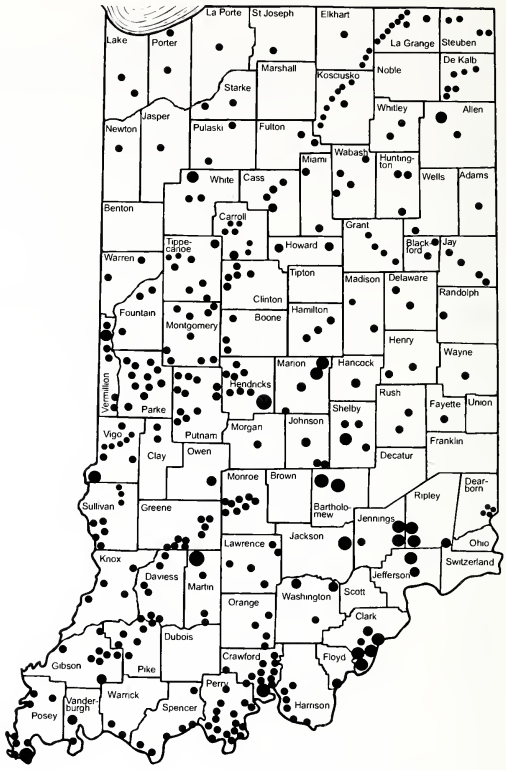

Figure 1.—Mist-netting for bats in Indiana, 1980 to present. Not all sites could be precisely designated. Large dots represent several to many nettings. Small dots sometimes represent more than one site.

METHODS

The data sets.—Only two sets of data (mist-netting and rabies lab) include all species of bats in Indiana. Other methods sample only certain species of bats. Mist-netting along streams or other flyways probably gives the best data for estimating numbers of individuals of each species. However, we do not have enough early (20–30 years ago) mist-netting data to compare with later data (1985 to present) to estimate population changes. Data from bats submitted to the Indiana Department of Health Rabies Laboratory are weighted towards bats that occur in buildings, but we separated the data by decade and thus looked for population trends. Therefore, we used the mist-netting data to estimate the numbers of the various species of bats living in Indiana; and the rabies lab data as our primary source (supplemented by other sources) to estimate population trends in the various species.

We have data from 1067 mist-nettings from throughout the state (Table 1; Fig. 1). Data are included here from 80 of the 92 Indiana counties, and from 6445 bats including all ten species currently known to exist in the state. This sample contains two major biases: oversampling at Prairie Creek in Vigo County, where the evening bat is abundant, and in Clark County where the only gray myotis colony occurs, clearly producing large counts for those two species in those two areas. To correct for this bias we calculated the average number (3.1) of evening bats per netting at Prairie Creek for three rather than the 181 nettings that occurred there [3.1 × 3 samples = 9 rath-

Table 1.—Bats caught in 1067 nettings from throughout Indiana. The estimated numbers here are derived on a proportional basis (ratio) using our big brown bat estimate of 1,111,360 individuals (see text). Data are adjusted downwards for a large number of nettings of *Nycticeius humeralis* in Vigo County, and of gray bats in Clark County by including average number in three samples for those species in those counties.

Species	Number netted	Ratio	Estimated number
Eptesicus fuscus	1748	1.000	1,111,360
Lasiurus borealis	1268	0.725	805,736
Myotis lucifugus	883	0.505	561,237
Pipistrellus subflavus	741	0.424	471,217
Myotis septentrionalis	741	0.424	471,217
Myotis sodalis	246	0.141	156,702
Nycticeius humeralis (658)	105	0.060	66,681
Lasiurus cinereus	70	0.040	44,454
Lasionycteris noctivagans	16	0.009	10,002
Myotis grisescens (74)	12	0.007	7,780
Myotis austroriparius	0	0.000	prob. extirpated
Corynorhinus rafinesquii	0	0.000	accidental
Total	5830		3,706,386

er than 562] and the average of 1.02 gray myotis per netting [1.02 × 3 = 3 rather than 65 gray myotis] for Clark County. These changes gave totals of 105 evening bats and 12 gray myotis, thus reducing the total from 6445 to 5830 bats (Table 1).

Whitaker & Gummer (2000) previously estimated the number of big brown bats in Indiana at 504,000. However, this was a very conservative estimate, and the actual number is clearly higher than that. We currently estimate the number of big brown bats in the state at 151 per colony × 80 colonies per county × 92 counties = 1,111,360. The 1748 big brown bats (Table 1) are 29.9% of the total bats (5830) netted, thus our estimate of 1,111,360 big brown bats represents 29.9% of the total bats in the state. From these data, we can estimate the total number of bats in the state at 3,706,386 (Table 1).

We assumed that bats mist-netted were taken in proportion to their relative abundance, then we estimated the number of bats for each species in the state based on its ratio to big brown bats. Data obtained this way are given in Table 1 listed in order by decreasing abundance of the bats.

The bats submitted to the rabies laboratory (Table 2) favors bats most apt to come into contact with humans (big brown bats and little brown myotis); but all ten species of bat currently living in Indiana were included, and most appear to occur in this sample in reasonable proportion to our overall assessment of their abundance using all sources of data. *Myotis septentrionalis* does appear to be under-

Table 2.—Bats submitted to rabies laboratory by decade, numbers and percent of total (in parentheses).

	1966–1969	1970–1979	1980–1989	1990–2000	Total
Eptesicus fuscus	473 (59.2)	1145 (70.6)	1495 (68.2)	1911 (68.4)	5024 (67.8)
Lasiurus borealis	184 (23.0)	313 (19.3)	428 (19.6)	447 (16.0)	1372 (18.5)
Myotis lucifugus	61 (7.6)	52 (3.2)	103 (4.7)	116 (4.2)	332 (4.5)
Pipistrellus subflavus	18 (2.3)	12 (0.7)	29 (1.3)	180 (6.4)	239 (3.2)
Lasiurus cinereus	30 (3.8)	47 (2.9)	44 (2.0)	51 (1.8)	172 (2.3)
Lasionycteris noctivagans	5 (0.6)	17 (1.0)	45 (2.1)	50 (1.8)	117 (1.6)
Myotis sodalis	15 (1.9)	13 (0.8)	27 (1.2)	21 (0.8)	76 (1.0)
Nycticeius humeralis	10 (1.3)	12 (0.7)	7 (0.3)	9 (0.3)	38 (0.5)
Myotis septentrionalis	3 (0.4)	11 (0.7)	11 (0.5)	8 (0.3)	33 (0.4)
Myotis grisescens	0 (0)	0 (0)	0 (0)	1 (0.04)	1 (0.01)
Total	799	1622	2189	2794	7404

Table 3.—Data on bats from netting as compared to that from the Indiana Department of Health Rabies Laboratory, Indianapolis.

	Netting			Rabies lab		
	Rank	No.	%	Rank	No.	%
Eptesicus fuscus	1	1748	29.9	1	5024	67.8
Lasiurus borealis	2	1268	21.7	2	1372	18.5
Myotis lucifugus	3	883	15.1	3	332	4.5
Pipistrellus subflavus	4	741	12.7	4	239	3.2
Myotis septentrionalis	5	741	12.7	8	33?	0.8
Myotis sodalis	6	246	4.2	7	76	1.0
Nycticeius humeralis	7	105	1.8	9	38	0.5
Lasiurus cinereus	8	70	1.2	5	172	2.3
Lasionycteris noctivagans	9	16	0.3	6	117	1.6
Myotis grisescens	10	12	0.2	10	1	0.01
Total		5830			7404	

represented. Only one gray myotis, taken in 2000, was included. However, this is logical since there is only one gray bat colony in the state and is increasing.

Other data sets give information on some species only. Data on bats hibernating in 52 caves, many of them inhabited in winter by *M. sodalis*, also provide information on *M. lucifugus*, *P. subflavus*, and *E. fuscus*. Data from trapping at cave and mine entrances provide information primarily on *M. lucifugus*, *M. septentrionalis* and *P. subflavus*. Data on bat colonies in buildings give information on *E. fuscus*, *M. lucifugus*, *P. subflavus* and *N. humeralis*.

RESULTS

We used mist-netting data to estimate the total number of each of the 10 species of bats currently existing in the state (Table 1), based on ratios with respect to the big brown bat. In order of decreasing abundance, they are *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis lucifugus*, *M. septentrionalis, Pipistrellus subflavus*, *Myotis sodalis*, *Nycticeius humeralis*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, and *Myotis grisescens*. Note that the estimates for *Myotis septentrionalis* and *Pipistrellus subflavus* are the same. *Myotis austroriparius* is probably extirpated, and *Corynorhinus rafinesquii* is best considered as of accidental or sporadic occurrence from Kentucky rather than as resident.

The best set of data for assessing population trends is that from the rabies lab (Table 2), and includes 7404 bats that have been identified. These numbers by decreasing overall abundance are: *Eptesicus fuscus* – 5024 (67.8%), *Lasiurus borealis* – 1372 (18.5%), *Myotis lucifugus* – 332 (4.5%), *Pipistrellus subflavus* – 239 (3.2%), *Lasiurus cinereus* – 172 (2.3%), *Lasionycteris noctivagans* – 117 (1.6%), *Myotis sodalis* – 76 (1.0%), *Nycticeius humeralis* – 38 (0.5%), *Myotis septentrionalis* – 33 (0.4%), and *Myotis grisescens* – 1 (0.01%). Only one gray myotis was in the rabies lab sample; and it was submitted in 2000, the last year of the study. This is logical, as the only known colony of gray myotis numbered 400 when first discovered in 1982, and has increased to about 4000 by the year 2000. A comparison of percentages of bats from netting and from the rabies lab is given in Table 3. Both sets of data indicate that *Eptesicus fuscus*, *Lasiurus borealis* and *Myotis lucifugus* are the three most abundant species of the state. However, *Eptesicus fuscus* accounts for about ⅔ of the bats in the lab sample, whereas it accounted for about ⅓ in the netting sample. This is explained by the fact that it is the most common house bat, and therefore most likely to be turned in to the rabies lab. The prominence of this species in the rabies sample depresses the percentages of all the other species. One might suppose that the little brown myotis would also be more abundant in the rabies sample than in the netting sample because it is the second most common bat in houses. It was not because it occurs in relatively few buildings as compared to the big brown bat. We found 330 big brown

bat colonies and only 58 little brown myotis colonies in buildings. Also (see below) it may be decreasing in abundance.

There are other notable differences between the netting and samples from the rabies lab. *Myotis septentrionalis* was particularly low in the sample from the rabies lab. The reason for this is difficult to explain as this species is quite common, as indicated by both netting and trapping cave and mine entrances. It would appear that the woodland habitat of this species, plus some behavioral peculiarity, keeps it from being often found by humans.

The occurrence of the silver-haired bat is more numerous in the rabies lab sample. This is because it migrates through Indiana in spring and fall, when less netting takes place. The abundance of the hoary bat in the sample from the rabies lab is somewhat difficult to explain. From netting, it appears to be relatively uncommon, but it may be relatively difficult to net. However, it is more likely that it is much more apt to be seen by people when it is sick and on the ground because it is large and showy.

Although the bats in the sample from the rabies lab occur in different relative proportions than those taken by mist-netting, they can be separated by decade and provide the best sample to determine if there are changes in proportions. Over time, such changes would indicate increases or decreases in relation to other species. Chi-square was used to test for significance, using the total numbers of bats taken in each period to calculate expected values.

It appears that *E. fuscus*, *P. subflavus*, and *L. noctivagans* have significantly increased over the period of the study in relation to the other species (X^2 = 10.78, 11.486, and 11.4 respectively, each with 3 *df*, $P = 0.05$). It appears that *L. borealis*, *L. cinereus*, *M. lucifugus*, and *N. humeralis* have decreased over this period in relation to the other species (X^2 = 20.1, 13.2, 24.5 and 13.7, again each with 3 *df*, $P = 0.05$). There was no evidence of a change in relative abundance to other species in the Indiana and northern myotis (X^2 = 9.4 and 4.7, each with 3 *df*).

Bats hibernating in caves and mines.—Five species of bats regularly hibernate in caves and mines in Indiana: the Indiana myotis, little brown myotis, northern myotis, eastern pipistrelle and big brown bat (Table 4). Data on bats hibernating in 28 caves visited numerous times from 1980 to the present are given in Table 4. These data are from Brack & Dunlap (unpubl. data), who have been conducting cave surveys of hibernating Indiana myotis and recording other species for the past 20 years. Note that little brown myotis and eastern pipistrelles are regularly recorded in many of the caves. However, only one individual of *M. septentrionalis* was recorded during all of this work, although it is common in Indiana, and it is commonly taken during trapping or mist-netting at cave entrances. For example, 291 individuals were trapped during 52 visits to assorted cave and mine entrances in Indiana along with 839 little brown myotis and 386 pipistrelles. Mumford & Whitaker (1982) did not know where *M. septentrionalis* hibernated. However, data collected since 1982, especially at Copperhead Cave in Vermillion County, plus mist-data, indicate that *M. septentrionalis* is seldom found hibernating in caves in Indiana because it nearly always hibernates in deep cracks and crevices (sometimes even in hollow stalactites), and thus is seldom seen (see *M. septentrionalis* account for more information). Of the estimated 1,111,360 big brown bats in the state, only about 15,000–30,000 individuals hibernate in caves and mines. The rest hibernate in buildings (Whitaker & Gummer 1993, 2000). This leaves us with three species of bats, *M. sodalis*, *M. lucifugus*, and *P. subflavus* for which we can get useful information from this source.

Winter cave counts give good estimates of Indiana myotis wintering in the state, as we think we know all major caves and most minor caves in which they hibernate. They are counted every other year and the count has increased from about 148,000 in 1981 to about 173,000 in 2001. Further, the count is fairly similar to the estimate obtained by the ratio of *M. sodalis* to *Eptesicus* during mist-netting, giving some degree of confidence in the netting estimates. The cave estimate applies only to winter, and we have no way of estimating how many of these bats remain in Indiana in the summer. Some probably migrate into Ohio and Illinois, and some form maternity colonies in Michigan. Also, some bats that winter in Kentucky summer in Indiana. Bats banded in Michigan have been

Table 4.—Bats hibernating in (52) caves in Indiana 1980–1999, average number per visit (mostly from Brack & Dunlap 1999). The asterisk (*) indicates a single visit only in 1982.

	No. visits	*Myotis sodalis*	*Myotis lucifugus*	*Eptesicus fuscus*	*Pipistrellus subflavus*
Clark County					
Indian	1	0	0	0	0
Crawford County					
Batwing	10	15,263.5	*1	*0	*11
B-B hole	1	0	156	0	9
Bentz	2	1.5	51	5	28
Easter Pit	1	0	108	0	7
Mellet Pit	1	0	0	0	1
Little Mellet Pit	1	0	0	0	0
Robinson Ladder	6	271.2	55.2	0	10.7
Saltpeter	8	497.6	157.3	7	28.9
Twin Domes	10	74,770	*0	*0	*0
Westerhof	1	0	0	0	3
Wildcat	7	31.7	394.4	0	36.7
Wyandotte	9/10	13,480.8	78.3	22.2	11.9
Greene County					
Ashcraft	3	17	129.7	1.3	6.7
Clyfty	8	298.4	252.1	7.6	99.3
Ray's	11	30,973.1	1,159.4	76	37.5
Sexton Springs	4/5	95.3	71	1.6	23.3
Harrison County					
Binkley's	1	84	197	0	17
Jughole	7	11,232	9.7	8.3	9.9
Little Jug Hole	1	0	1	0	7
Parker's Pit	8/7	1,097.5	186.7	5.6	8.6
Penny Well	1	0	0	0	2
Swinney	2	20	1.5	6.5	0.4
Wallier	5	272.6	3.2	23.6	11.6
Lawrence County					
Bronson's	1	0	0	0	3
Dixon's Pit	1	0	133	5	75

Table 4.—Continued

	No. visits	*Myotis sodalis*	*Myotis lucifugus*	*Eptesicus fuscus*	*Pipistrellus subflavus*
Donaldson's	1	0	0	2.5	3
Donnehue's	2	0	108.5	8.5	8
Hamer's	1	0	1	10	1
King	2	0	0	2	0
Mitchell Crushed Stone	2	20	279	193	52
Salts	2	0	67.5	15.5	30
Sullivan	1	0	0	0	0
Twin	1	0	0	1	0
Martin County					
Aunt Liz	1	0	1	0	41
Granny's	1	0	1	0	14
Monroe County					
Big Windy (Bauer's Blowhole)	1	0	24	0	1
Borden's Pit	1	0	13	0	26
Buckner's	9	143	25.3	2.2	9.6
Coon's	10	3,129.9	235.6	2.8	134.8
Eller's	1	0	0	0	3
Grotto	10	2,922.1	690.1	2.1	24.4
King Blair/Brinegar's	5	416.8	401	0	151.8
Leonard's Spring	6	99	174	0.3	59.7
Ranard School	1	0	0	8	0
Salamander	4	18.8	100	0.3	37.5
Saltpeter	7	131.3	42.6	19.9	9.1
Owen County					
Boone's	1	0	1	10	18
Washington County					
Endless	7	247	569.3	12.9	52.9
Mill	1	0	9	0	74
Panther/Neyman	3	136.3	257.3	3.3	6.7
River	4	28	249	2.5	89.5

found at hibernacula in Indiana and Kentucky (Kurta et al. in press).

The cave counts give less accurate estimates of little brown myotis because not all caves are included, sometimes not even the entire cave in which counts are made. The cave counts were established for *Myotis sodalis*. However, many or most of the more important *Myotis lucifugus* hibernacula are included, and thus they may indicate population trends. *Myotis lucifugus* has been decreasing in Ray's Cave. This is particularly interesting because *Myotis sodalis* had been increasing in Ray's Cave until in 1999 when it harbored the most Indiana myotis of any cave throughout its winter range. (It dropped back into second in 2001.) The only other cave in which *M. lucifugus* might have been declining is Salamander, but there are too few data from Salamander to consider this a trend. In addition, periodic flooding has probably caused some loss of bats there. On the other hand there are three caves (Grotto, Coon and Endless) in which *M. lucifugus* may have been increasing. Indiana myotis may have increased a bit in Endless Cave, but they show little if any change in the other two caves. The only other cave we know of with numbers of either of these species is Copperhead Cave (a mine in Vermillion County) which usually contains about 200 little brown myotis and 100 pipistrelles.

Trapping at cave entrances.—Trapping and mist-netting at cave and mine entrances can give useful information on *Myotis lucifugus*, *M. septentrionalis*, *Myotis sodalis* and *Pipistrellus subflavus*. These three species are the common bats that swarm at cave and mine entrances, and hibernate in caves in Indiana. *Myotis lucifugus* and *M. septentrionalis* can be taken by netting entrances even in winter, *Pipistrellus* is seldom taken in winter. More data are needed, but *Myotis sodalis* appears to be uncommon at entrances except at caves in which it hibernates. Unfortunately, we have no caves or mines where we have extensive earlier and later data on any of these species.

Myotis lucifugus was the most common bat at Copperhead, Zenas, Donnehues and Wyandotte Caves. However, *M. septentrionalis* was most abundant at Panther Cave and was more abundant than *M. lucifugus* in 52 mines netted.

Bats roosting in buildings.—Data on bats roosting in buildings in Indiana are given in Table 5. The bats roosting in buildings in order of decreasing abundance are *E. fuscus*, *M. lucifugus*, *P. subflavus*, *N. humeralis*, and *M. septentrionalis*. Cope et al. (1961) collected information on 188 colonies in 1959; 30 years later Whitaker & Gummer (1993) collected information on 401 colonies. These data provide information on the relative, not absolute, numbers of bat colonies of these species in buildings. During this time the percentage of *E. fuscus* and *P. subflavus* colonies increased, whereas those of *M. lucifugus* and *N. humeralis* decreased. The individual species are discussed below.

Table 5.—Bat colonies in buildings in Indiana in 1989 as compared to 1959.

	Cope 1961 1959		Whitaker 1989	
	No.	%	No.	%
Eptesicus fuscus	142	75.5	330	82.3
Myotis lucifugus	41	21.8	58	14.5
Pipistrellus subflavus	1	0.5	12	2.9
Nycticeius humeralis	4	2.1	1	0.2
Total	188		401	

Southeastern myotis, *Myotis austroriparius*.—Mumford & Whitaker (1982) indicated that this species had decidedly decreased between 1949 and 1982. Most Indiana records are from hibernating individuals in caves. There were about 50 individuals in Bronson's Cave 7 February 1949 (40 were collected on the following day). The largest number recorded after that in Bronson's Cave was 8 on 30 March 1966. A cluster of 25 was found in Donaldson's Cave on 23 November 1951, and about two-thirds of them were banded. Since then, the maximum number seen in that cave was 3, on 6 March 1954. This species regularly hibernated in Donnehue's Cave at Bedford (Lawrence County), through the early 1970's. The number of individuals found there was 9 on 8 January 1954, 19 on 12 February 1955, and 28 on 28 December 1955. Small numbers of this species were found there as well as in a few other caves throughout the early 1970's. Twenty-five individuals were taken at Donnehue's Cave in 20 mist-nettings in 1970–71, mostly in August (10) and September (9). The last verified record of this species was one banded by J.B. Cope in Don-

nehue's Cave on 4 February 1977. This species appears to be extirpated in Indiana.

Gray myotis, *Myotis grisescens*.—Only one gray myotis was submitted to the rabies lab, and only 12 were taken by mist-netting, indicating the low number of gray myotis in Indiana. Only one (or possibly two) colony of this species in Clark County is known from the state. The gray myotis has increased from about 400 individuals in that colony in 1982 to nearly 4000 by the year 2000. Highest estimates for various years are: 1982 (400), 1986 (453), 1988 (253), 1990 (481), 1991 (752), 1994 (1101), 1997 (1949), 1998 (1552), 1999 (1430), 2000 (3768).

Little brown myotis, *Myotis lucifugus*.—Data from the rabies lab indicate a decrease in little brown myotis in relation to big brown bats and pipistrelles. Cope et al. (1991) found that little brown myotis colonies in buildings decreased in relation to big brown bat colonies between 1959 and 1989 (Table 5). *Myotis lucifugus* colonies decreased from 21.8% of the colonies in 1959 to 14.5% in 1989. Big brown bat colonies increased from 75.5% of the colonies in 1959, to 82.3% in 1989. If 82.3% of the colonies in buildings are of *E. fuscus* and if there are 80 big brown colonies per county, then there are about 80 × 92 or 7360 *E. fuscus* colonies in the state. The 58 little brown myotis colonies form 17.6% of the number of big brown bats. Following that logic, there should be about 0.176 × 7360 or 1295 little brown myotis colonies in the state. The average size we derived from 52 little brown myotis colonies (range from 6–6500) was 564, thus our estimate of little brown myotis in the state would be 564 × 1295 or 730,380. This is close to the estimate of 561,237 that we got as the ratio of bats of this species taken by mist-netting. Additional evidence that the little brown myotis has decreased is that besides the changes in proportion, two of the roosts that contained little brown myotis three decades ago now contain big brown bats (Cope et al. 1991). Our data indicate a decrease in little brown myotis in Indiana.

Northern myotis, *Myotis septentrionalis*.—*Myotis septentrionalis* was estimated by mist-netting to be fourth or fifth in relative abundance (total 471,217). Because little is known about its biology it is difficult to assess population trends. It hibernates in caves and mines; but very few individuals can be found, even in caves known to serve as hibernacula. Mumford & Whitaker (1982) stated that although they had found the species hibernating in at least 20 caves, the greatest number of individuals found during one visit was 11 in a cave near Kent (Jefferson County) on 3 January 1959. Usually there were not more than 6 per cave, although numerous bats of this species may be found swarming at certain cave entrances. Whitaker & Rissler (1992) found that *Myotis septentrionalis* apparently hibernates in Copperhead Cave in some numbers, although none have been found there during hibernation. Evidence indicating that Copperhead Cave is a hibernaculum is: (1) the number of northern myotis that enter the cave in fall; (2) the number that emerge in winter and spring; and (3) on relatively warm spring nights, when northern myotis are emerging from the mine, individuals can be found exiting from the cracks. For example, 12 were observed on 15 March 1991. Some of these bats had smears of mud on them, apparently indicating recent emergence from cracks.

Whitaker & Rissler (1992) used trapping data to estimate the number of northern myotis emerging from Copperhead Cave in spring. Sampling times averaged 7.5 h or 62.5% of the dark period at that time of year. To determine if banded bats might be reentering the mine or if bat activity might taper off after our normal sampling period ended, bats were trapped throughout the night on two separate occasions. The results indicated that bat activity continued all night and that individuals seen earlier did not generally return to the mine after our normal sampling period ended. The emergence of northern myotis in 1990 started 9 March and lasted through 17 April, a total of 40 nights. Trapping was done on ten of these nights. The average number of northern myotis taken per night was 22.7 (4.2 bats/0.625 = 22.7 bats; SD = 15.9, SE = 5.3). Based on this number, an estimated 908 northern myotis exited the mine in spring (22.7 bats/night × 40 nights = 908). This figure is a tentative, minimal estimate of the hibernating population there.

Cave and mine netting in fall and other mist-netting data indicate that this species, *M. lucifugus* and *P. subflavus* are relatively similar in number, and that it is probably about the fourth or fifth most abundant bat in the state. Interestingly, very few northern myotis,

M. septentrionalis, totalling only 33, or 0.4%, are submitted to the rabies laboratory. It is not known why so few bats of this species are submitted to the rabies laboratory other than it probably has something to do with its behavior. All other data indicate that the species is remaining reasonably stable in the state.

Indiana myotis, *Myotis sodalis*.—The best data on *M. sodalis* are those currently collected every two years in hibernacula, and the population has increased somewhat during this period. The five caves in Indiana currently serving as primary hibernacula for Indiana myotis are included in Table 4. Overall, numbers of hibernating Indiana myotis have increased in Wyandotte, Jug Hole and especially in Ray's Cave. Ray's Cave had become the most important hibernaculum for *M. sodalis* in its entire range in 1999. However, the number there decreased in 2001, when Twin Domes Cave was again the top hibernaculum for that species in Indiana. However, range-wide, this species appears to be decreasing, especially in Kentucky and Missouri. Suitable temperature (3–7°C) appears to be the single most important factor necessary for the success of hibernating Indiana myotis (Richter et al. 1993), although temperature stability is also important. In Indiana, Indiana myotis have apparently been moving from Batwing and Twin Domes Caves. The temperature in Batwing and Twin Domes Caves may have been increasing (due to global warming?) whereas temperatures in Wyandotte and Ray's Caves have decreased (due to modifications at entrance in Wyandotte allowing cold air in, and due to the increased size of a natural opening of a small upper entrance in Ray's Cave, causing movement of warm air upward and out, and thus pulling cold air in the lower main entrance). Bat numbers have radically increased in these two caves, which has led to the statewide increase.

Big brown bat, *Eptesicus fuscus*.—The best evidence for the big brown bat population trends is the data from the rabies lab and the data on bat colonies in buildings. We estimate that there are about 1,111,360 big brown bats present in Indiana. Assuming a bat to forage out 1.5 miles (2.4 km) in all directions from its colony, we might assume a foraging range of $3 \times 3 = 9$ square miles (23 sq km). Since an average county in Indiana includes about 750 square miles (1920 sq km), then there might be about 80 colonies per county (750/ $9 = 83.3$). Evidence that the big brown bat is increasing is that the number submitted to the rabies lab is increasing proportionately, forming 59% of the total in 1966–69, nearly 70% later (Table 3). This is the bat species most adapted to living alongside man, and is the species most often in structures. We believe that big brown bats are increasing and that they are tending to outcompete little brown (and evening) bats for roosts in buildings. The mist-netting data also show that the big brown bat is the most common bat of the state, although the number taken by netting (1268) is lower than expected. This is probably because big brown bats are most abundant near structures, and most of the samples were along wooded streams rather than near structures.

Eastern pipistrelle, *Pipistrellus subflavus*.—Data from the rabies lab indicates numbers and percentages of this species have been increasing considerably, from 2.3% in 1966–69 to 6.4% in 1990 to 2000 (Table 2). Also, the pipistrelle increased as a percentage of colonies found in buildings, up in 1989 at 2.9% from 0.5% 30 years earlier (Cope et al. 1991). *Pipistrellus subflavus* was estimated by mist-netting along with *M. septentrionalis* to be fourth/fifth in relative abundance.

Evening bat, *Nycticeius humeralis*.—The evening bat was the seventh most abundant bat as estimated by mist-netting (Table 1), with its revised count being 105. All earlier evening bat colonies were found in buildings, but recently we have found evening bats to be abundant in hollow trees in bottomland woods in the Wabash Valley from Vigo to Posey County (but not east in the Ohio River Valley). We think that *Nycticeius* was present all along in this habitat, and that this habitat resembles the original prime habitat for the species at least in the northern part of its range. Further, we suspect that *Eptesicus* and *Nycticeius* may compete for roosts in buildings and that *Eptesicus* has basically won out in this competition in upland areas. For example, 4 among 188 (2.1%) of the bat colonies found in buildings by Cope et al. (1961) were evening bat colonies. The original colonies were all gone by 1993 when only 1 of 401 (0.2%) colonies then was of *Nycticeius*. Because of its loss in buildings and from loss of bottomland woods, we suspect that this species has decreased in Indiana since the 1960's.

Silver-haired bat, *Lasionycteris noctivagans*.—Few silver-haired bats are taken by mist-netting, but most of our netting is after the spring migration and before the fall migration of this species. A relatively large number of specimens are submitted to the rabies lab, 117 over the years, and data from that source indicate that this species is increasing slightly.

Red bat, *Lasiurus borealis*.—The red bat appears to be the second most abundant bat in the state (after the big brown bat), as indicated by both mist-netting and rabies lab data. However, the rabies lab data indicate a decrease in this species relative to other species. From the rabies lab, the numbers of bats submitted continue to increase (indicating increased awareness of bats in the state). However, the percentage of red bats has shown a significant decline from 23.0% of the bats in 1966–69 to 16% in the last decade. We suspect that the decrease in the numbers of red bats is real and is related to continued loss of natural lands, especially woodlands, to development.

Hoary bat, *Lasiurus cinereus*.—The rabies lab data show significant decrease in percentage of hoary bats submitted through time. The hoary bat formed 3.8% of the bats submitted in 1966–69, as compared to 1.8% in the past decade. The decrease in the number of hoary bats, like the red bat, is probably related to continued loss of natural lands, especially woodlands, to development.

Rafinesque's big-eared bat, *Corynorhinus rafinesquii*.—There are only 18 records of this species known in the state. We consider it of accidental occurrence from Kentucky and Illinois. The earliest record of this species in the state was from Putnam County where two individuals were taken in 1894 in a cave near Greencastle (Butler 1895). Otherwise, there are 10 records for the Spring Mill State Park area (1902–1907), five in Washington County (1954–1962), and one in Tippecanoe County (1959). The last verified records of this species in the state had been in 1962 in a cave near Smedley in Washington County. However, a big-eared bat was reported from Squire Boone Cave several times over a period of about a month in the summer of 1992.

DISCUSSION

In this paper we have estimated the number of bats of the various species currently living in the state. These estimates are based on assumptions which we cannot adequately assess, particularly those with regard to the big brown bat. Errors in the values for that species of course translate to errors in the other species. However, we are relatively satisfied with our assumptions and our results. We think that they do give a fairly good idea of bat populations in Indiana and that they should provide baseline data for future estimates, either from additional mist-netting or from bats from the rabies laboratory.

The best individual estimates of the total number of individuals of a species are for the Indiana myotis (about 173,000 bats from the 2001 winter counts), and the gray myotis (3700+ from summer emergence [dusk] counts). Thus, these species can be used as a test of the method used below. Our estimate from netting is that Indiana myotis represent about 14.1% of the total capture and when compared to big brown bats, gives an estimate of 156,702. This is relatively close to the number hibernating in caves (173,000) in Indiana, which gives some measure of confidence to these estimates. The difference observed, about 17,000 bats, may be because not all bats that hibernate in Indiana spend the summer in Indiana. Some summer in Michigan (Kurta et al. in press) and we suspect some summer in Ohio and Illinois. The rest probably summer in Ohio, Michigan and Illinois. The gray myotis estimate was 7780 as opposed to about 3700 gray myotis by dusk counts, or about twice the estimate. We did not feel this difference was excessive given the way the estimate was obtained, the small number of gray myotis in the sample, and that only one colony of gray myotis was involved.

ARE BATS DECLINING?

It appears to us that Indiana myotis, gray myotis, big brown bats, and eastern pipistrelles have increased in Indiana, whereas red bats, hoary bats, evening bats, and little brown myotis have declined over the last four decades. It is difficult to determine the status of the northern long-eared bat and the silver-haired bat. The southeastern myotis has been extirpated, and Rafinesque's big-eared bat should be considered of only accidental occurrence in Indiana.

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LITERATURE CITED

Brack, V., Jr. & K. Dunlap. 1999. Winter survey for Indiana bats, *Myotis sodalis*, in hibernacula of Indiana. Final Report, Indiana Department of Natural Resources, Indianapolis. 73 pp.

Butler, A. 1895. The mammals of Indiana. Proceedings of the Indiana Academy of Science 4: 81–86.

Cope, J.B., W.W. Baker & J. Confer. 1961. Breeding colonies of four species of bats of Indiana. Proceedings of the Indiana Academy of Science 70:262–266.

Cope, J.B., J.O. Whitaker, Jr. & S.L. Gummer. 1991. Duration of bat colonies in Indiana. Proceedings of the Indiana Academy of Science 99: 199–201.

Kurta, A., S.W. Murray & D. Miller. In press. Indiana bats: Journeys in space and time. *In* Indiana Bats: Biology and Management of an Endangered Species (A. Kurta & J. Kennedy, eds.). Bat Conservation International, Austin, Texas.

Mumford, R.E. & J.O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press. Bloomington. 537 pp.

Richter, A.R., S.R. Humphrey, J.B. Cope & V. Brack, Jr. 1993. Modified cave entrances – Thermal effect on body mass and resulting decline of endangered Indiana bats, *Myotis sodalis*, in southern Indiana. Conservation Biology 7: 407–415.

Tuttle, M.D. & J. Kennedy. 1999. Indiana bat hibernation roost evaluation. Phase II. Results from the first annual cycle. Bat Conservation International. 11 pp. plus appendices.

Whitaker, J.O., Jr. & S.L. Gummer. 1993. The status of the evening bat, *Nycticeius humeralis*, in Indiana. Proceedings of the Indiana Academy of Science 102:283–291.

Whitaker, J.O., Jr. & S.L. Gummer. 2000. Population structure and dynamics of big brown bats (*Eptesicus fuscus*) hibernating in buildings in Indiana. American Midland Naturalist 143:389–396.

Whitaker, J.O., Jr. & L.J. Rissler. 1992. Seasonal activity of bats at Copperhead Cave. Proceedings of the Indiana Academy of Science 101:127–134.

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Walter, J. 1992. The significance and complexity of communication in moths. Pp. 25–66, *In* Insect Communications: Mechanisms and Ecological Significance. (P.N. Work & J.S. Rivers, eds.). Princeton University Press, Princeton, New Jersey.

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